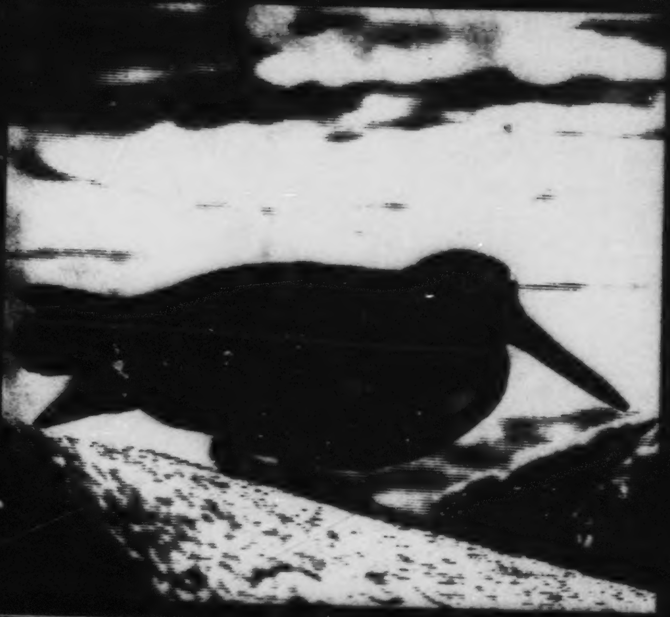
Kees Vermeer
Robert W. Butler
(editors)

The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia

A special publication
compiled by the
Canadian Wildlife Service
for the Pacific Northwest Bird
and Mammal Society



Proceedings of a symposium
sponsored by the
Pacific Northwest Bird and
Mammal Society and the
Canadian Wildlife Service,
held in Sidney, BC,
11 December 1987

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Robert W. Butler[2]
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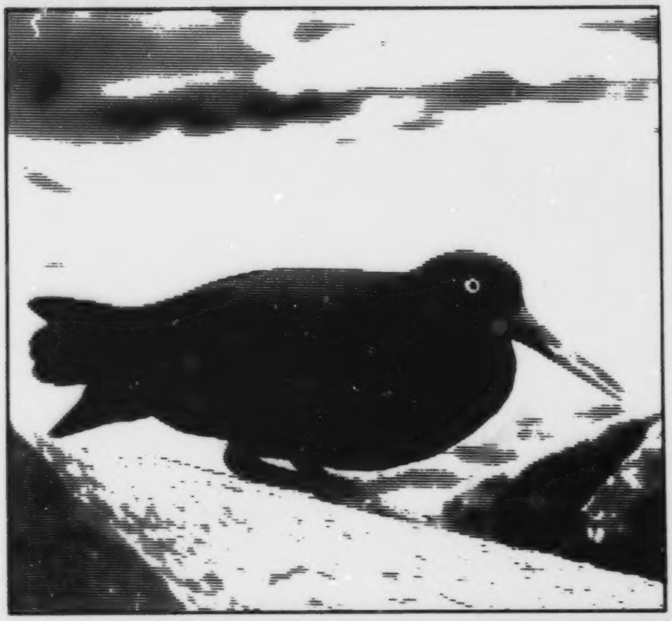

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Introduction

Kees Vermeer and Robert W. Butler

This book presents the proceedings of a symposium on the ecology and status of marine and shoreline birds in the Strait of Georgia and adjacent waters. The symposium was held on 11 December 1987 at the Institute of Ocean Sciences, Sidney, BC. The objective of the symposium was to combine various disciplines to provide a review of what is currently known about the marine biology of the Strait of Georgia ecosystem, with particular emphasis on birds.

The proceedings of a previous symposium (Parsons 1983) did not include information on marine and shoreline birds, despite the fact that such birds occupy the highest trophic levels of the aquatic food chain in the strait. To complement that symposium, we invited experts from several fields—physical oceanography, botany, invertebrate biology, fisheries, and ornithology—to participate in a multidisciplinary symposium that we hoped would provide a better overview of interactions between birds and their environment than would a symposium given by ornithologists alone.

Although its sections vary in scope and depth, this book nevertheless provides the most recent overview of what is known of marine and shoreline birds and their environment in the Strait of Georgia. Many of the authors identify important gaps in knowledge in their particular fields and advance suggestions as to how these insufficiencies can be remedied. We believe that these proceedings will become an important reference for educators, biologists, and ornithologists, as well as for researchers, fieldworkers, and managers in resource management. We hope that the recommendations in the individual papers will be acted upon by decision makers in a timely fashion.

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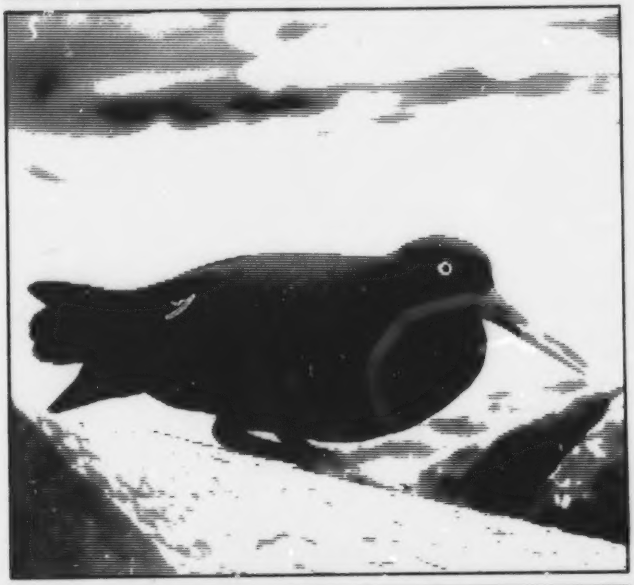
Parsons, T.R. 1983. Symposium on the Fisheries and Oceanography of the Strait of Georgia. Can. J. Fish. Aquat. Sci. 40:1025.

Part 1

The physical and biological environment and prey organisms



Physical oceanography of the Strait of Georgia as related to marine birds

Paul H. LeBlond

1. Abstract

The physical oceanography of the surface waters of the Strait of Georgia is reviewed, with particular emphasis on those patterns of water properties and currents that are pertinent to the lives of marine birds.

2. Résumé

L'auteur présente un aperçu de l'océanographie physique du détroit de Georgia et met particulièrement l'accent sur les propriétés de l'eau et les courants caractéristiques qui se rapportent à la vie des oiseaux marins.

3. Introduction

In this paper, I present an overview of the physical oceanography of the Strait of Georgia as it pertains to the life of a marine bird. As it is the state of the sea surface and its upper layers that is of most interest to seabirds, I restrict my discussion to the near-surface waters of the Strait of Georgia, mentioning deep waters only inasmuch as they affect surface properties. This review is thus limited in scope; broader surveys of the water motions and properties of the Strait of Georgia have been presented elsewhere (Waldichuk 1957; LeBlond 1983). Thomson (1981) wrote a popular introduction to the oceanography of the BC coast that also presents an excellent qualitative description of the properties of the Strait of Georgia. A comprehensive survey of all available data sources in physical oceanography pertinent to the Strait of Georgia and other southern BC waters was compiled by Lemon and Kowalski (1982). Reviews of biological oceanographic aspects of the strait were prepared by Harrison *et al.* (1983) and Levings *et al.* (1983) for pelagic and benthic domains, respectively. Waldichuk (1983) presented a recent review of pollution in the Strait of Georgia.

The basic physical mechanisms determining the properties of the waters of the Strait of Georgia and their general seasonal and spatial variations are reviewed in Section 4 of this paper, which provides an essential background for the presentation to follow. Particularly sensitive or interesting areas from a seabird's point of view are then identified and examined in Section 5. A short summary is presented in the last section.

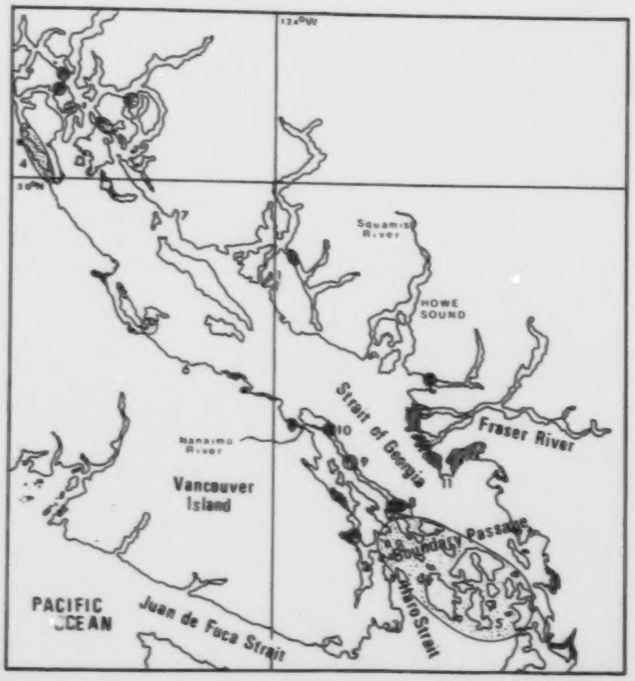
4. The prime movers

Three physical processes dominate the physical oceanography of the Strait of Georgia: freshwater runoff, tides, and winds. By themselves and through their interactions, they determine the spatial and temporal distributions of currents and water properties.

4.1. Freshwater runoff

The Strait of Georgia is an estuary—a semienclosed coastal area of the sea that receives significant freshwater runoff. By far the most important source of fresh water entering the strait is the Fraser River (Fig. 1), which accounts for more than 80% of the total runoff (LeBlond *et al.* 1983). The output of the Fraser River is seasonally variable. A strong freshet due to the melting of snow in

Figure 1
The Strait of Georgia. Areas of extensive tidal flats are shown cross-hatched; regions of intense tidal streams are indicated by stippling. (1) Sakinaw Lake; (2) Saanich Inlet; (3) Victoria; (4) Discovery Passage; (5) Rosario Strait; (6) Qualicum; (7) Powell River; (8) Active Pass; (9) Porlier Pass; (10) Gabriola Pass; (11) Point Roberts.



British Columbia's mountainous interior occurs in early summer. Peak discharge occurs between late May and early July and reaches a rate of up to 25 000 $m^3 \cdot s^{-1}$. In contrast, winter runoff, between November and March, can be as low as 1400 $m^3 \cdot s^{-1}$. There is also considerable interannual variability in the intensity and timing of the freshet, related mainly to the amount of snowfall in the preceding winter and to the rate at which it melts in the early summer.

Light fresh water issuing from the Fraser River flows over the denser salt water of the southern Strait of Georgia, spreading in a thin (5–15 m) brackish plume easily identified by its silt content (Fig. 2). The plume waters gradually mix with the salty waters below them as they flow away from the river mouth. Tides and wind mixing contribute to this process. The near-surface density stratification associated with freshwater runoff thus decreases in strength with distance from the river mouth. The presence of a thin layer of brackish silty water at the surface of the Strait of Georgia has important consequences on surface dynamics. Because of the sharp density contrast (or pycnocline) between the surface layer and the salty water below it, vertical mixing is inhibited. Because of its turbidity, the upper layer absorbs most of the incident sunlight, leading to enhanced warming, which reinforces the density stratification. In addition, the presence of a strongly stratified upper layer creates favourable conditions for the generation of fronts and internal waves.

Suspended sediments give the plume its distinctive colouration, ranging from a milky white colour through a range of pale browns and greens. Particulate matter gradually settles out of the plume waters as they flow seawards; the sediment concentration is also decreased by mixing with clear salt water. On the scale of the whole Strait of Georgia, the plume appears as a graded pattern of colour, passing sometimes gradually, but often stepwise, from a very muddy hue near the river mouth to a deep blue at the northern and southern ends. The processes of mixing and sediment settling occur simultaneously, so that the salinity of the surface waters increases as their colour shifts towards that of clean seawater. Although there is no known direct quantitative relationship between salinity and colour in the Strait of Georgia, it is possible to estimate relative salinities of adjacent waters by comparing their colours (Fig. 3). Sharp fronts are also readily identified by an abrupt change in water colour. Whether birds can recognize such features is an interesting question.

As in all estuaries (Dyer 1973), the surface flow of fresh water seawards induces a return flow of salt water at depth, which is called the estuarine circulation. Near the source of freshwater outflow, this circulation has an important vertical component, associated with the phenomenon of entrainment, which contributes to the initial dilution of the plume and to its enrichment in dissolved nutrients. Entrainment describes the process whereby a relatively quiescent fluid (the deeper salty water) is dragged along and incorporated into a more turbulent flow (the surface plume). The effect of entrainment on the dynamics of the Fraser River plume has been examined by Cordes *et al.* (1980); its influence on surface concentrations of phytoplankton has been noted by Parsons *et al.* (1969). The mid-strait maximum in phytoplankton and zooplankton observed in the Strait of Georgia (Fig. 4) is in part a consequence of the vertical nutrient flux into the surface layer as a result of entrainment near the river mouth, as discussed by de Lange Boom (1976).

Figure 2
The Fraser River plume. This is a negative print of a LANDSAT image. The sediment-laden runoff from the Fraser River's many mouths is clearly visible, as is that from the Squamish River at the head of Howe Sound (centre top).

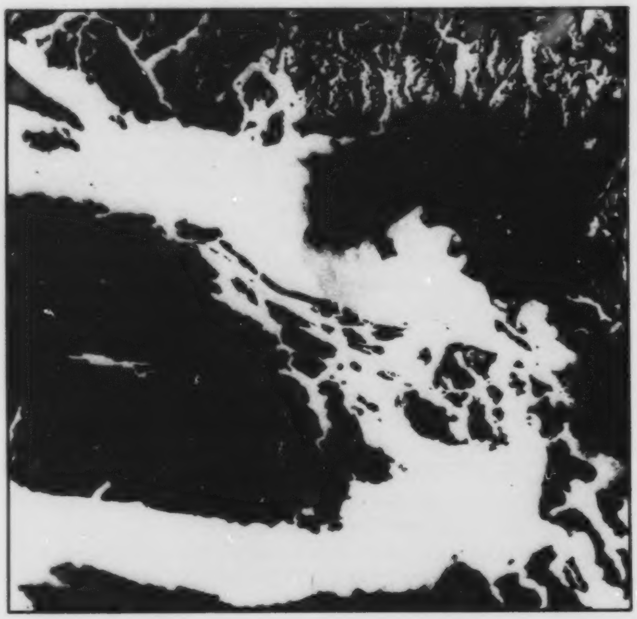
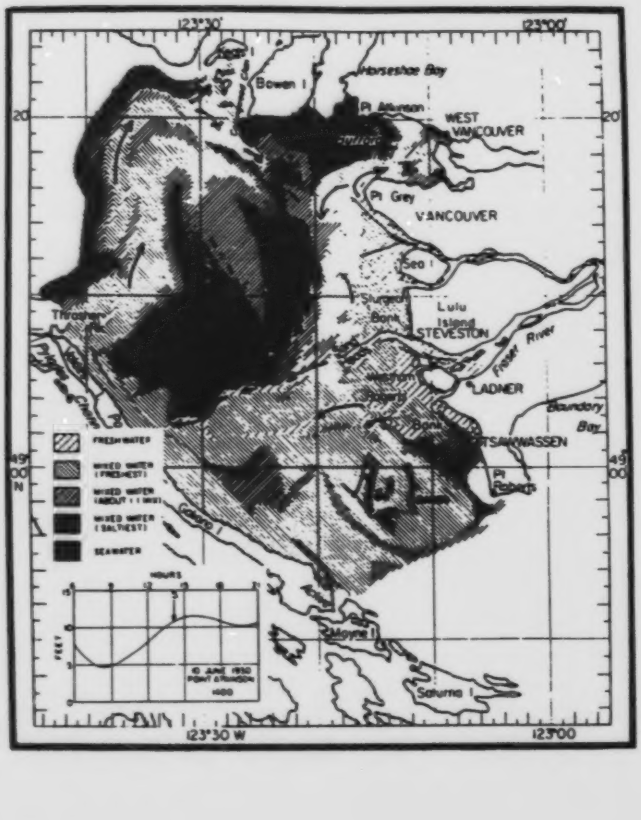
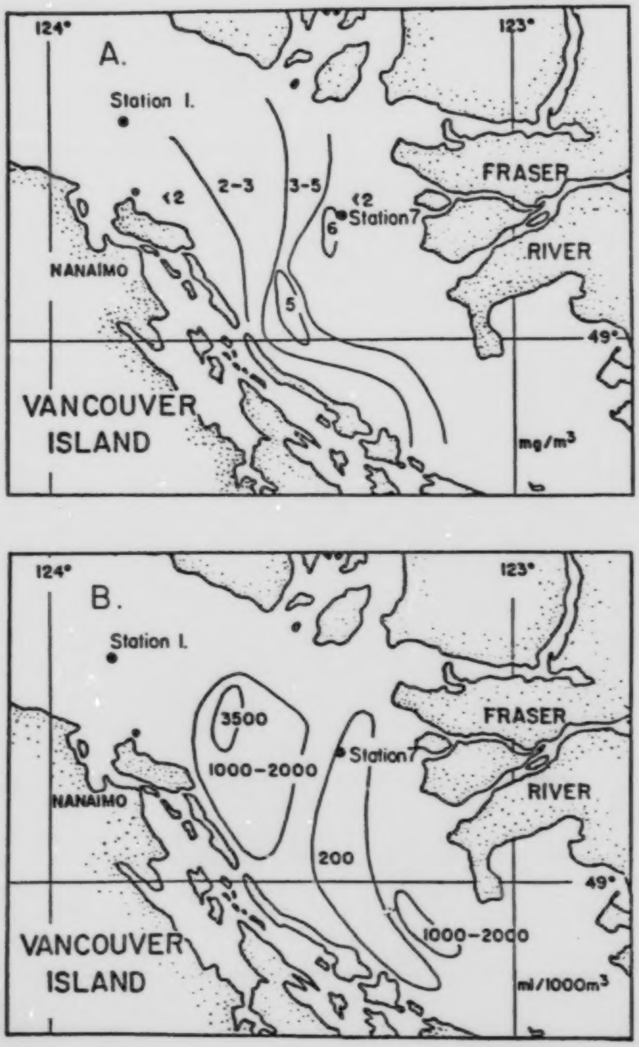


Figure 3
Distribution of water masses at the surface of the Strait of Georgia, inferred from observed silt distribution. The effect of the flood tide in carrying fresh, sediment-laden water northwards is clearly visible (from Tabata 1972).



The estuarine circulation draws in oceanic water at depth from beyond the confines of the Strait of Georgia, contributing to the renewal of deep waters, to their reoxygenation and replenishment in dissolved nutrients, and thus eventually to the total productivity of the estuary. Because the salt water entrained into the plume does not come from great depths, deep-water replacement has at most an indirect effect on surface properties. Even if the deeper waters of the Strait of Georgia were to alter their properties significantly, perhaps to the point of becoming anoxic, it is probable that the surface properties might not be affected at all. The Black Sea, for example, which is anoxic below about 150 m, supports fisheries and abundant sea life in its upper stratum (Tolmazin 1985*a*, 1985*b*). On a smaller but more relevant scale, Saanich Inlet and Sakinaw Lake—the former an inlet in contact with the sea in the southern approaches to the Strait of Georgia, the latter a now-isolated body of water cut off from contact with the strait by isostatic rebound of the land—both have normal upper-layer sea life above an anoxic lower layer (in Saanich Inlet, from 100 to 150 m [Herlinveaux 1962]; in Sakinaw Lake, below about 30 m [Northcote and Johnson 1964]). With this perspective in mind, I suggest that deep-water processes are of little relevance to the environment of seabirds, most of which would not dive down to the levels where anoxic waters are found.

Figure 4
Chlorophyll *a* (A) and zooplankton (B) distributions in the central Strait of Georgia (from Parsons *et al.* 1969)



Although lesser rivers contribute only a small fraction of the total runoff into the Strait of Georgia, their influence on water properties in the immediate vicinity of their mouths may be considerable and overshadow that of the more remote Fraser River. Thus, whereas the massive runoff from the Fraser River will affect water properties over most of the Strait of Georgia, conditions in the vicinity of smaller estuaries (e.g., near the mouth of the Nanaimo River or at the head of Howe Sound near the Squamish River) will vary in response to the runoff from the local rivers. In most of these cases, the catchment basin lies entirely within the coastal area, and runoff responds more immediately to precipitation than in the Fraser River. The discharge of coastal streams shows a peak during the rainy season (late fall - early winter) and sometimes, depending on how much snow falls in the catchment basin, a second peak during early summer.

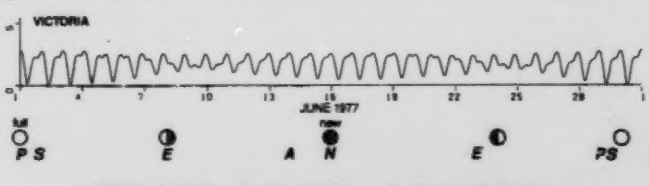
4.2. Tides

The tide is the principal, as well as the most predictable, contributor to sea level and current variations in the Strait of Georgia. It is well known that ocean tides are a response to the gravitational effects of the moon and the sun. However, in small coastal basins such as the Strait of Georgia, the tide is more a response to the tides of the adjacent ocean than to direct astronomical forcing.

The tidal influence propagates from the sea into the Strait of Georgia through the Strait of Juan de Fuca in the south and Queen Charlotte Sound in the north (Crean 1976). Tidal ranges vary from a maximum of about 5 m at the northern end of the Strait of Georgia to a low of about 4 m at its southern entrance, near Boundary Passage. These large tidal ranges are responsible for the presence of an extensive intertidal zone in gently sloping areas of the shore. Such areas are favoured by shorebirds; they will be identified below.

The character of the tide is mainly semidiurnal, with two high and two low waters per day, generally with important diurnal inequality (Fig. 5). Near Victoria, the diurnal constituent of the tide dominates, and there is only one high and one low water level per day. Exposure of the intertidal zones thus varies from day to day as the tide changes, to different degrees in the different areas of the Strait of Georgia according to the nature of the tide.

Figure 5
Tidal sea-level variations at Point Atkinson (near Vancouver) and Victoria. The phases and declinations of the moon are also shown (from Thomson 1981).

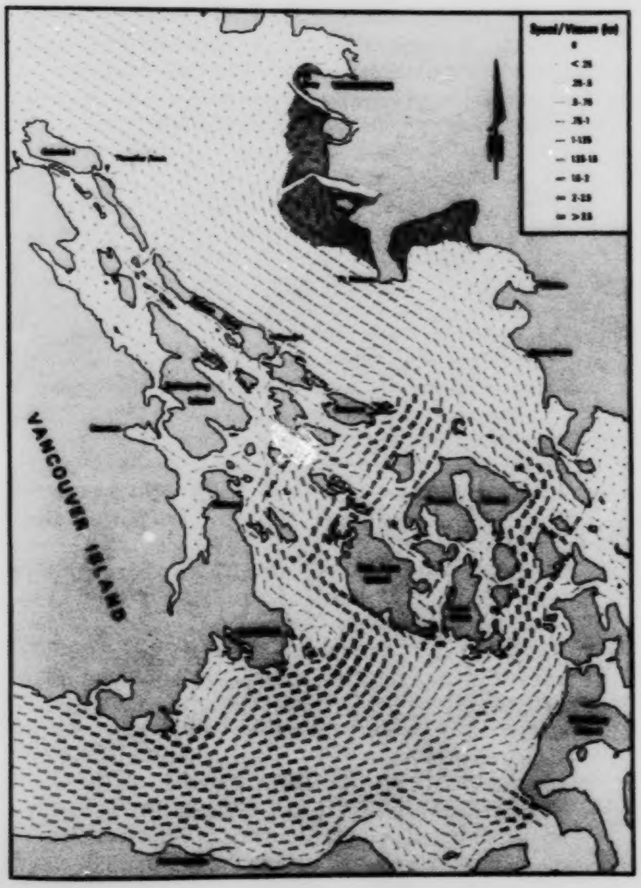


Tidal currents are the dominant flows in the Strait of Georgia. They are strongest in constricted passages connecting the strait to the Pacific Ocean, as well as between islands and obstructing headlands in the strait itself. An atlas of tidal currents based on Crean's (1976) numerical modeling work is widely available (Canadian Hydrographic Service 1983). An example of the resolution that it provides is illustrated in Figure 6.

Tides contribute significantly to vertical mixing, especially where tidal currents are strong. Sharp transitions occur between stratified regions, where the brackish upper-layer outflow from the Fraser River (or locally from some smaller stream) forms a stable upper layer, and well-mixed regions, where tidal currents destroy the density stratification. These transitions are called "fronts"; they shift back and forth with the ebb and flow of the tide over regions where estuarine and tidal influences strive for dominance. There is normally a sharp salinity difference across a front, usually accompanied by a significant change in suspended sediment concentration. Fronts are thus readily identified from the air because of the contrast in water colour across them.

Simpson *et al.* (1977) introduced an index that characterizes the relative importances of tidal mixing and stratification. This index is defined as $E = H/u^3$, where u is the speed of the tidal current and H the water depth. Small values of E are characteristic of waters that are well mixed vertically and result from strong currents and/or shallow depths. Large values of E typify stratified regions. Transition areas from large to small E (the exact values depending on the region) are frontal zones and are recognized as particularly productive from a biological point of view.

Figure 6
Tidal currents at flood tide in the southern Strait of Georgia (from Canadian Hydrographic Service 1983)



4.3. Winds

Meteorological forcing—more specifically the wind—is the third important factor influencing water properties. Winds create waves and surface currents and cause vertical mixing. Surf and wave breaking affect the environment of the marine bird; wave action in the nearshore region increases water turbidity and may thus affect the hunting efficiency of diving birds. In deeper water, on the other hand, where wave action does not reach the bottom, vertical mixing of the surface brackish layer with saltier, sediment-free water below decreases its overall turbidity and reduces its density contrast. Longshore currents induced by waves carry sediments, flotsam, and dissolved substances with them from one area of the shoreline to another, causing erosion, deposition, and advection of nutrients or pollutants. The wind also causes motion of the upper layer, pushing it along in the direction in which it blows at about 3% of the wind speed (Huang 1979). The resulting advection may cause upwelling, which brings up colder, nutrient-rich water from below and affects local water temperature as well as productivity. Regions of frequent wind-driven upwelling are particularly rich in marine life. An instance of wind-induced coastal upwelling that may be directly related to bird populations has been discussed by Schneider and Methven (1988).

4.4. Interactions

The combined actions of river runoff, wind, and tides lead to a temporally and spatially varying pattern of currents and water properties. A brief overview of the seasonal variability is presented now; details, particularly of the spatial variation, are examined in the next section of this paper, with special attention to phenomena of relevance to birds.

Meteorological and oceanographic conditions in the Strait of Georgia differ sharply between winter and summer, although the two blend into each other during fall and spring transition periods. During summer (May–October), winds are often northwesterly, because of a large-scale high-pressure system offshore that is also accompanied by clear skies and high insolation levels (Kendrew and Kerr 1955; Hay and Oke 1976). Runoff is at a maximum, freshet occurring in the Fraser River and other mainland rivers between late May and mid-July. The surface waters of the Strait of Georgia are turbid, warm, and of low salinity; surface stability is high. In contrast, winter meteorological conditions are dominated by the recurring arrival of low-pressure systems from the Pacific Ocean, with strong southeasterly winds, cloudy skies, and heavy precipitation. Runoff from the Fraser River is at a minimum; surface waters are clear, cold, and salty. An occasional brief (a week or so) outbreak of polar air flowing over the mountains sometimes brings clear skies, freezing temperatures, and snow flurries to the coast.

The contrast between winter and summer characteristics of surface water properties is seen in Figures 7 and 8. Winter surface temperatures are lower than those of summer and also much more uniform over the whole Strait of Georgia. The surface salinity is strikingly lower during the summer over a wide area extending out from the

Figure 7
Distribution of water properties at the surface of the Strait of Georgia in February 1950: (A) salinity (ppt); (B) temperature (°C) (from Waldichuk 1957)

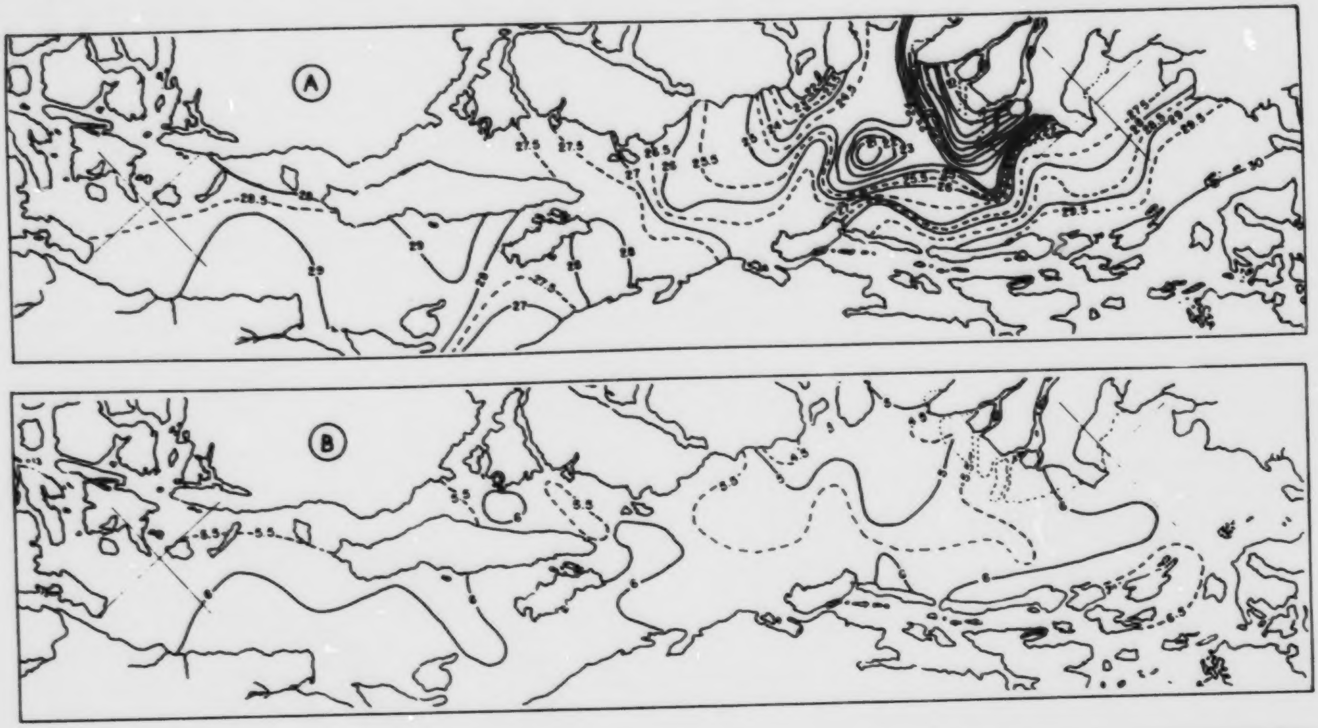
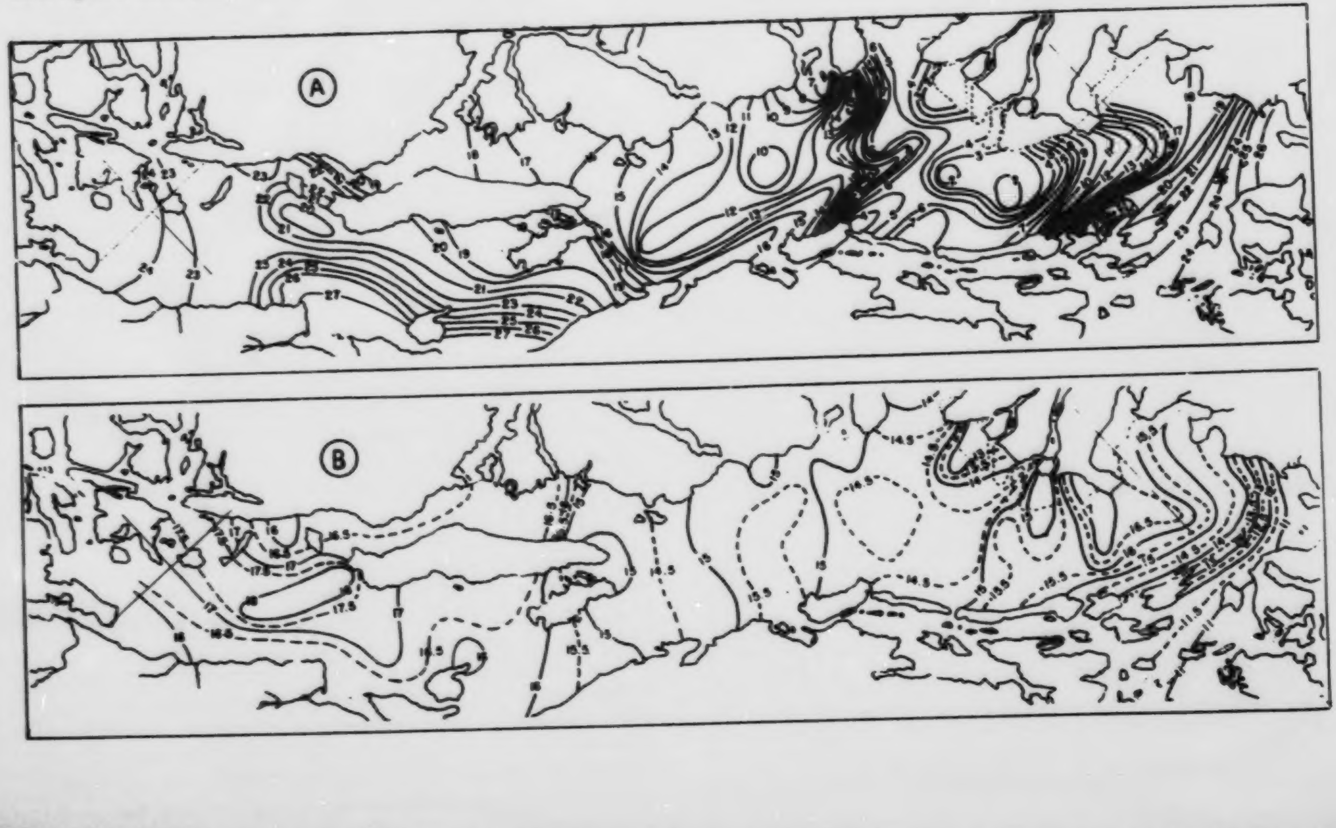


Figure 8
As in Figure 7, but for June 1950



mouth of the Fraser River; a similar seasonal contrast is seen at the mouths of smaller rivers.

5. Phenomena of interest to birds

A cursory survey of recent literature on relationships between marine birds and their physical environment provided guidance in assessing relevant phenomena in the Strait of Georgia (Brown 1980; Kinder *et al.* 1983; Hunt and Schneider 1987; Schneider *et al.* 1987).

In terms of the scales of variability distinguished by Hunt and Schneider (1987), the phenomena occurring in a coastal basin such as the Strait of Georgia all lie within the coarse (1–100 km) and fine (1–1000 m) scales. Coarse-scale phenomena are associated with meteorological or estuarine forcing of similar scales; the finer-scale phenomena are determined by the shape of the shoreline or that of the bottom, or by sharp transitions in water properties at fronts.

5.1. Coarse-scale phenomena

I have already noted the strait-wide effects of Fraser River outflow in determining the stability and turbidity of the upper layer, as well as its seasonal variability. It is unlikely that the presence of a strong pycnocline would have a direct effect on the activities of seabirds. A density contrast of 15 units in sigma-tee in 1 m (de Lange Boom 1976; Cordes *et al.* 1980), typical of the sharpest transition between the plume and the underlying salt water, corresponds to a relative change in density of 15 $kg \cdot m^{-3}$ in 1015 $kg \cdot m^{-3}$, i.e., less than 1.5%. It is improbable that diving birds would be affected by such small changes in buoyancy. Surface stratification will, however, have important indirect effects on the determination of regions of biological productivity and thus of higher abundance of marine animals. A strong stratification prevents vertical mixing and hence the replenishment from below of nutrient substances exhausted by near-surface phytoplankton demand. Beyond a restricted area near the mouth of the Fraser River, where substantial entrainment brings salty, nutrient-rich water from below into the upper layer, the latter is essentially isolated from the subjacent waters. Transition areas, at the edge of the plume, will thus present sharp contrasts in biological productivity because of changes in the availability of nutrients from below (Harrison *et al.* 1983). One would thus expect that the wide areas covered by the freshwater plume during its strongest and widest manifestation might not be as rich in sea life as those parts of the Strait of Georgia that surround it.

In contrast to the strong stratification found in the central Strait of Georgia, extensive regions of narrow and shallow passages where vertical homogeneity is the norm are located at its northern and southern extremities. The dimensions of these passages also place them within the category of "coarse" features. In Discovery Passage in the north, Haro and Rosario straits in the south, and the complex of channels surrounding the southwestern Gulf Islands in the west, one finds vertically mixed regions, tens of kilometres in horizontal extent, where turbidity and salinity are, respectively, lower and higher than in the central Strait of Georgia. Sea life in the tidal and intertidal zones is enormously richer, a fact apparent even to the casual beachcomber (Levings *et al.* 1983). The transition between stratified and mixed areas was explored by Parsons *et al.* (1981) and is clearly illustrated using the Simpson mixing index referred to above (Fig. 9).

Synoptic weather patterns—the low- and high-pressure systems that bring overcast and clear skies, respectively, to the coast—affect atmospheric conditions over the whole Strait of Georgia and are thus to be counted among coarse-scale environmental features. As noted above, there is a strong seasonality in meteorological conditions. On a smaller but still coarse scale, according to the earlier definition, one finds a few areas of special weather conditions associated with prominent landforms. In the mainland coast inlets (e.g., Howe Sound and Jervis Inlet), incursions of polar air seawards are an occasional winter feature, often an advance warning of massive arrival of polar air masses on the coast. Such "Squamish" winds are strong and turbulent and carry very cold air (Tyner 1951; Schaeffer 1975). Squamish-type winds are well known in other parts of the world (e.g., the Mistral in southern France and the Bora in the northern Adriatic). Reid (1981) discussed a well-documented case of cold air outflow through Cascade Mountain passes in western Washington State. The strong, bitterly cold Squamish winds would be among the worst environmental conditions encountered by seabirds.

During warm summer weather, winds in coastal fjords regularly alternate in a diurnal cycle characterized by strong landward (up-inlet) sea breezes building during the day to a maximum in late afternoon and calming gradually in the evenings. At night, as the land cools, a land breeze develops in the opposite direction (down-inlet). Land breezes are usually not as strong as sea breezes. The presence of mountain slopes on the sides and at the head of fjords tends to enhance the strength and gustiness of cool nighttime land breezes. Birds might be able to take advantage of these winds to move up and down coastal inlets.

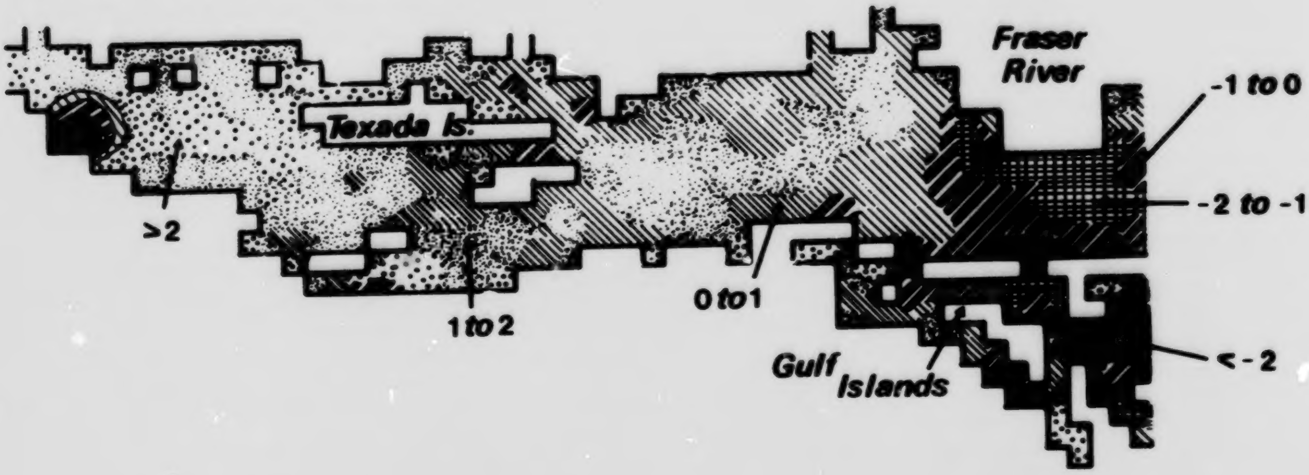
On the Vancouver Island side of the Strait of Georgia, an irruption of air from the Pacific Ocean across the Alberni gap in the island's mountainous backbone causes the Qualicum winds, which create strong cross-strait winds between Qualicum and Powell River during otherwise quiet summer high-pressure conditions.

5.2. Fine-scale phenomena

Fine-scale phenomena include a variety of fronts, localized upwelling areas associated with the shape of the coastline or of the bottom, zones of surface convergence associated with internal waves and Langmuir cells, and inherent biological patchiness.

Estuarine fronts are found at the junction of the freshwater plume and the salty water beyond. They occur near the mouths of all rivers entering the sea. The outflow of the Fraser River is modulated by tidal changes in sea level in the Strait of Georgia: during ebb tide, the discharge of fresh water is at a maximum; during flood tide, the river is pushed back, and no fresh water reaches the strait. The freshwater discharge thus pulsates with the rhythm of the tide. At each ebb, water of sharply contrasting properties spreads over the strait; an estuarine front separates it from its surroundings. The plume waters gradually mix with salt water entrained from below, so that at the next ebb they have become saltier and less silty than the newly arriving freshwater pulse and find themselves on the seaward side of a new estuarine front. At any one time, many estuarine fronts are observed in the Strait of Georgia, each separating water released during a different ebb. These fronts are advected by the tide and eroded by mixing; they separate water masses identifiable by their turbidity (see above, Fig. 3).

Figure 9
Map of the stratification index $E = H/u^3$ in the Strait of Georgia. Here, H is the water depth and u a typical tidal current speed. Values of log E are plotted. Light shades (log $E > 0$) correspond to strong stratification; dark shades are well-mixed areas (log $E < 0$) (from Parsons *et al.* 1981).



Stronach (1977) observed and interpreted estuarine fronts found near the mouth of the Fraser River. The strongest fronts occur on the flood tide, when the salt water is pushed under the lighter brackish layer. Estuarine fronts are swept back and forth by tidal currents, advancing and retreating with the ebb and flow and being sharpened or attenuated through mixing by wind or tide. Fronts are regions of strong surface convergence where surface waves are amplified; their frequent association with the rising tide has earned them the name of "tide rips." Concentrations of flotsam are found at estuarine fronts; as some of this flotsam may be edible, marine birds are often attracted to fronts. The principal frontal regions are found near the main tidal channels connecting the Strait of Georgia to the sea and near the mouths of rivers entering it.

The transition between strongly stratified and vertically mixed waters that occurs on the periphery of the Strait of Georgia is a tidal frontal region. Estuarine fronts may reach that region on the ebb tides, only to be swept back inwards on the flood. The entrances of the narrow passages that allow access to the strait (Haro and Rosario straits in the south, Active, Porlier, and Gabriola passes on the west, and Discovery and other passages in the north) are all regions of strong diurnal or semidiurnal variations, particularly intense during the freshet and spring tide periods. Because these passages are not only narrow but also shallow, they are also the site of strong topographic upwelling, where the deeper waters are brought to the surface by being forced over a shallow sill. Mixing is intense, and organisms from the whole water column are stirred up to the surface. Very dense concentrations of seabirds are found in those areas. Active Pass in particular is well known for its concentration of seabirds (Vermeer *et al.* 1987).

Another kind of front occurs at the junction of convergent currents in the lee of a headland. This type of front is visible as a line of surface debris trailing off the headland in the direction of the flow. It may also be observable through changes in water colour associated with a concentration of suspended sediment. Such a front is often seen south of Point Roberts on the ebbing tide.

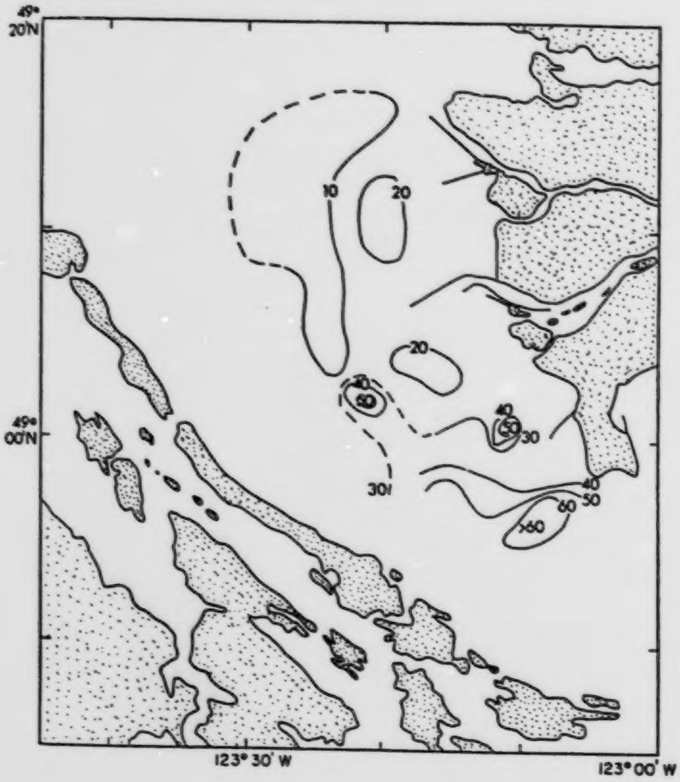
The interface between the brackish upper layer and the denser, underlying salt water is an abrupt pycnocline that, when disturbed, will radiate internal waves in the same way as the sharp density interface between water and air will support surface waves. The flood tide pushing back estuarine fronts is the main source of internal disturbances and generates regular groups of internal waves. Through nonlinear dispersion, these waves gradually evolve into trains of long-crested solitary waves propagating into the centre of the Strait of Georgia. These waves are from tens to hundreds of metres in length and of periods from 1 to 10 min; they travel at a speed of about 2 $\text{km}\cdot\text{h}^{-1}$ and are particularly noticeable in the southern part of the strait, between Boundary Passage and the mouth of the Fraser River. Internal waves are oscillations of the pycnocline about its equilibrium depth and cause very little surface displacement. They are, nevertheless, readily detected from above through their interactions with shorter surface waves. Alternating zones of convergence and divergence associated with internal oscillations affect the steepness of surface waves. They create, in turn, alternating zones of ruffled and smooth waters at the surface, which are readily detected from the air because they reflect light differently. Internal waves thus appear as bands of light and dark water from the air. In the strongest waves, there is some accumulation of flotsam in traveling convergence zones; this may attract scavengers of all types, including birds.

Langmuir (1938) noticed how flotsam tended to line up at the water surface in bands parallel to the wind direction and described a circulation—Langmuir cells—consisting of a helicoidal drift of near-surface water particles. Several theoretical explanations have been put forward to explain the generation of Langmuir cells (e.g., Leibovich 1983). Langmuir cells are most clearly seen in shallow lakes. At sea, wind waves are larger and surface line delineations harder to detect visually, but acoustic measurements (D. Farmer, Institute of Ocean Sciences, pers. commun.) suggest their presence even in heavy seas. The concentration of flotsam by Langmuir cells may facilitate the task of foraging birds.

Biological patchiness is also known to occur in an otherwise homogeneous environment as a result of the interaction of oceanic turbulence and the internal dynamics of plankton growth (Denman and Powell 1984; Mackas *et al.* 1985). Patchiness may also arise through behavioural habits of mobile organisms, a common example being that resulting from fish schooling. Observations of chlorophyll *a* in the plume show some striking patchiness (Fig. 10). The specific origins of phytoplankton concentrations remain mysterious; the question of why they occur at all on the scales observed, let alone precisely at a specific location on a particular day, is still unanswered. Whereas the relationship between fish schooling and bird concentrations is direct and evident, that between phytoplankton patches and bird distribution is much more indirect and thus more difficult to document with confidence.

A final fine-scale effect of particular relevance to marine and shoreline birds is that of the nature of the coastline itself. Much of the shoreline of the Strait of Georgia is steep and rocky. There are a few areas of wide beaches and extensive tidal flats and marshes in the vicinity of river mouths (shown by hatching in Fig. 1), and these harbour considerable bird populations (Vermeer 1983).

Figure 10
Chlorophyll *a* patchiness (units of mg · m⁻³) in the area of the Fraser River plume (from de Lange Boom 1976)



6. Conclusion

There are by now well-explored links between some oceanographic situations and bird concentrations. However, there remain some serious gaps in the understanding of how specific marine environmental conditions may affect the ecology of seabirds. It is still not within the state of the art to predict, even on a climatic basis, the geographical distribution of seabird populations in a particular region entirely on the basis of the characteristics of the physical environment. At the most fundamental level, the relationship between local productivity and environmental factors is not sufficiently well understood. Even though some of the basic principles have become clear, predictive application to specific locations remains unreliable. As it is not yet possible to understand the spatial distribution and variability of the birds' food source, it is equally beyond us to predict where birds will live. The situation is, of course, not entirely hopeless. There are areas of the sea that are known to be more productive than others; one need not start at the bottom of the ladder, with the physical environment, to explain where seabird populations ought to be found. However, even from that intermediate starting point, the relationship between environment and population geography is not entirely clear. Much remains to be done to understand why birds live and congregate where they do.

7. Acknowledgements

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Distribution and aggregation of zooplankton in the Strait of Georgia and their potential availability to marine birds

David L. Mackas and John D. Fulton

1. Abstract

The Strait of Georgia and adjoining inlets contain a highly productive marine ecosystem. Spatially and seasonally averaged zooplankton biomass and secondary productivity are large compared with those in most oceanic regions, and the zooplankton are clearly important intermediate links in the food web leading to marine birds. Despite the large amount of zooplankton produced in the Strait of Georgia, direct feeding on zooplankton by seabirds seems to be relatively rare. The primarily planktivorous species are rare or absent on the inner coast, and planktivory appears to be an opportunistic rather than an obligate feeding strategy. We have therefore concentrated on the special behavioural and environmental factors that on occasion make a subset of the total zooplankton community in the Strait of Georgia highly available to avian predators.

2. Résumé

Le détroit de Georgia et les petits bras de mer adjacents contiennent un écosystème marin très productif. La moyenne spatiale et saisonnière de la biomasse du zooplancton et la productivité secondaire sont élevées comparativement à celles de la plupart des régions océaniques, et le zooplancton est sans aucun doute un chaînon intermédiaire important de la chaîne alimentaire qui mène aux oiseaux marins. En dépit de la grande quantité de zooplancton produite dans le détroit de Georgia, il semble assez rare que les oiseaux de mer s'en nourrissent directement, ce qui fait contraste avec la situation sur la côte extérieure de la Colombie-Britannique. Les espèces essentiellement planctophages sont rares ou absentes sur la côte intérieure, et il semble que les oiseaux se nourrissent de plancton occasionnellement plutôt que par obligation. Nous nous sommes donc particulièrement intéressés aux facteurs comportementaux et environnementaux en raison desquels, occasionnellement, une partie de la quantité totale de zooplancton présente dans le détroit de Georgia est facilement accessible aux oiseaux prédateurs.

3. Introduction

Zooplankton occupy a crucial position in the marine food web that supports marine birds. Except in very shallow water, zooplankton are responsible for nearly all the conversion of plant to animal biomass. The trophic coupling to seabirds is direct: some seabirds, especially the tubenoses and auks, use zooplankton directly as food; most other seabirds feed primarily on planktivorous fish and epibenthic invertebrates. Ashmole (1963), Furness and Birkhead (1984), and Birt *et al.* (1987) argued that size and fledging success rates of seabird breeding colonies may be limited by prey depletion in the vicinity of the colonies. Links between plankton and seabird distributions have been noted in a variety of oceanographic regions.

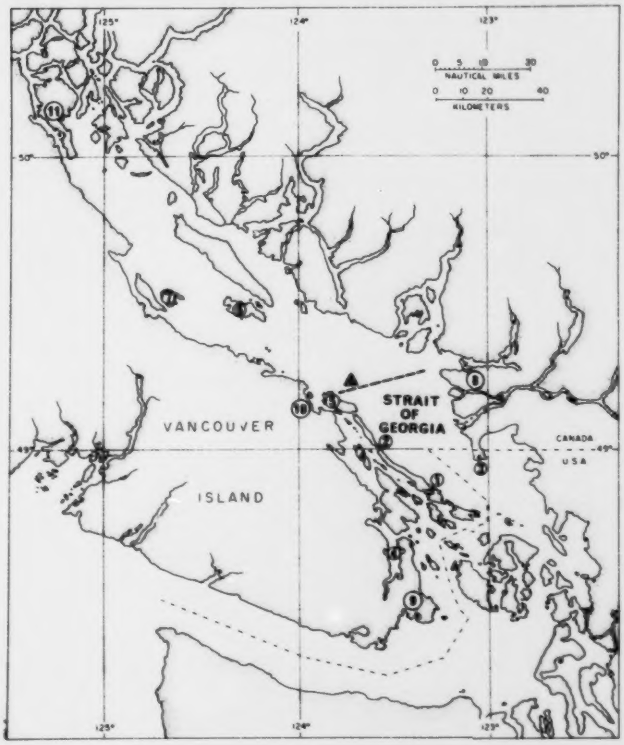
In this paper, we examine the distribution and productivity of zooplankton in the Strait of Georgia (for locations, see Fig. 1) and their potential importance to resident and migratory marine bird populations. We quote frequently from a recent review of the biological oceanography of the Strait of Georgia and adjoining inlets by Harrison *et al.* (1983)—especially for the description of larger-scale spatial and seasonal productivity and biomass patterns—which gives a comprehensive overview of the very large body of biological oceanographic work done prior to the early 1980s. We place our major emphasis on factors affecting the local availability of plankton to birds and to the small fish eaten by birds.

Vermeer (1983) noted that, in contrast to the outer BC coast, exclusively or primarily planktivorous marine birds are rare on the inner coast. Birds that feed on zooplankton in the Strait of Georgia seem to do so opportunistically rather than routinely. Past studies have amply demonstrated that BC inner-coast waters produce large amounts of high-quality organic matter each year. For seabirds and other marine predators, the usefulness of the Strait of Georgia as a feeding ground is set, not by the overall productivity of the system, but by how this productivity is packaged and by how accessible the highest concentrations are to a given predator. Within the general topic of plankton availability, we therefore consider components such as vertical distribution (seabirds feed at or near the sea surface rather than at depth), size distribution (large zooplankton are more readily detected by visual predators), spatial aggregation (dense patches of prey, once located, are more easily exploited), and the interaction of the zooplankton distributions with dominant time scales of variability (especially the daily, tidal, meteorological, and seasonal cycles) in the physical environment.

4. Methods

Much of the information presented in this paper is a review of existing literature; readers should consult the cited sources for methodological details. We present new data on macrozooplankton distributions, diel vertical

Figure 1
Chart of the Strait of Georgia showing major landmarks and locations discussed in this paper: (1) Active Pass; (2) Porlier Pass; (3) Point Roberts; (4) Saanich Inlet; (5) Gabriola Island; (6) Lasqueti Island; (7) Hornby Island; (8) Vancouver; (9) Victoria; (10) Nanaimo; (11) Quadra Island. Filled triangle marks the sampling site for the vertical migration data shown in Figure 4. Dashed line marks transect sampled for copepod aggregation at the margin of the Fraser River plume (Fig. 5).



migration, and small-scale near-surface aggregations. Large-scale horizontal distribution of macrozooplankton (Figs. 2 and 3) was sampled in 1981 during an ichthyoplankton survey of the southern Strait of Georgia (Mason *et al.* 1984). An 80-station grid was sampled every three weeks between February and June. At each station, daytime vertically integrating oblique tows were taken from near bottom to surface with a Bongo net (0.25-m^2 mouth area, 0.35-mm black Nitex mesh). Diel vertical migration patterns (Fig. 4) are described from a 24-h time series of stratified samples taken with a 0.25-m^2 BIONESS multiple net sampler. Surface patchiness of copepod abundance at the Fraser River plume margin is described from results of continuous flow-through sampling with an electronic particle counter (Mackas and Louttit 1988).

5. Zooplankton species composition and seasonal cycle

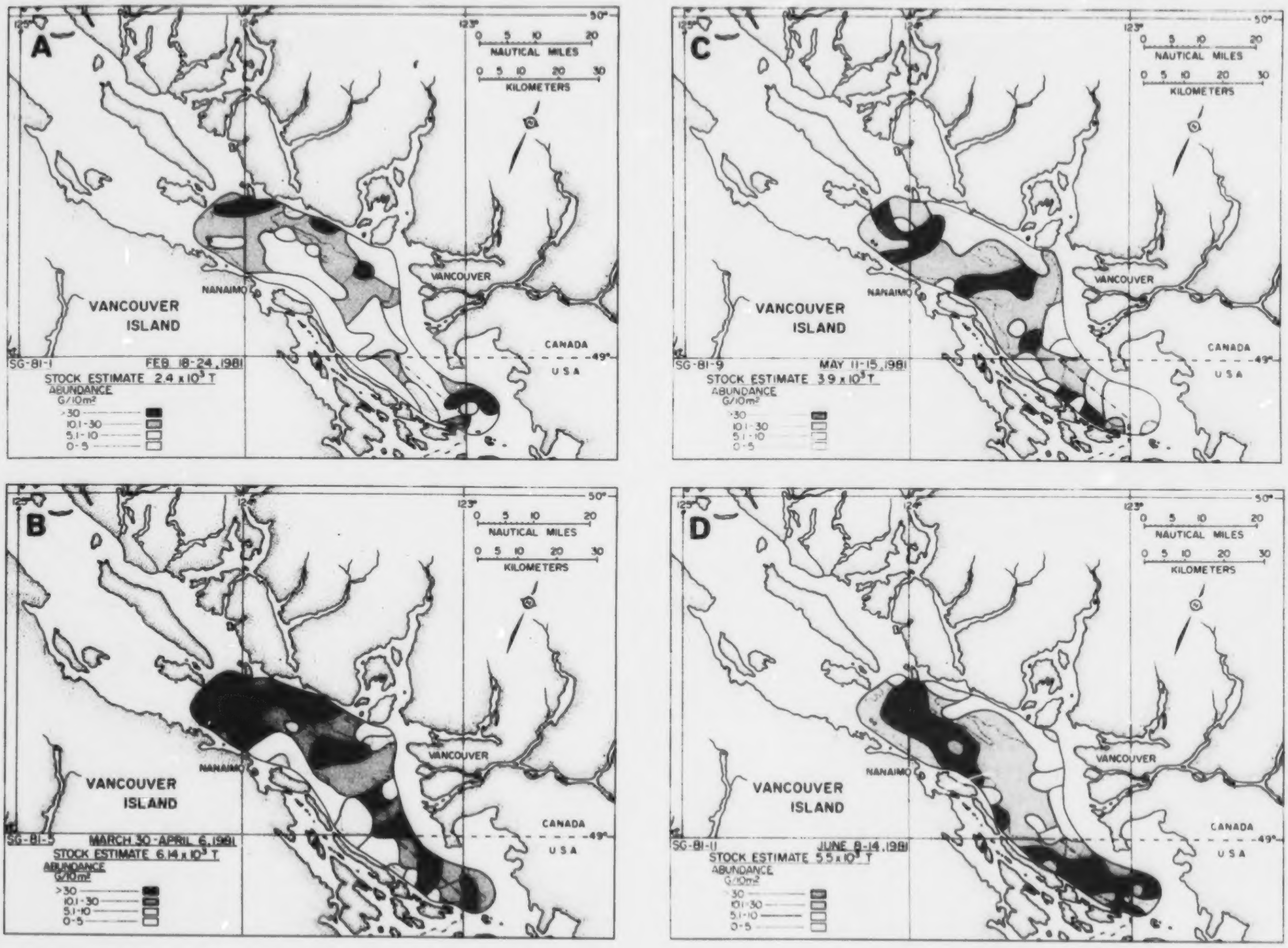
The composition of the near-surface zooplankton community varies considerably over the annual cycle and spatially between the main body of the Strait of Georgia and the shallower of the adjoining bays and inlets. In this section, we examine the abundance of species in various locations at different times of year. The discussion is largely taken from Harrison *et al.* (1983) but includes some reinterpretation based on more recent data.

In the winter generally, and throughout the year in shallow waters, the near-surface zooplankton are dominated by small (<2 mm total length) copepods. Because of their low visibility, these animals are unlikely to be preyed upon directly by birds; however, they do serve as prey for larger zooplankton and small fishes (especially larval and juvenile life stages). Nearshore regions also contain occasional high concentrations of meroplanktonic larvae, such as barnacle nauplii and crab zoeae and megalopae. These are both larger and more brightly pigmented than the small copepods, but they are only briefly abundant, usually in spring and early summer when water transparency is reduced by phytoplankton and riverine sediment inputs. Healey (1980) discussed the considerable importance of this nearshore community as prey for juvenile salmonids.

In areas where bottom depths exceed about 200 m, a single species, the large (4- to 5-mm body length) herbivorous copepod *Neocalanus plumchrus*, dominates the upper 20–50 m of the Strait of Georgia from April through early June. This species shows a strong seasonal vertical migration (Fulton 1973) and is absent from the surface layer for the remainder of the year. In mid-May, population densities average about $(1\text{–}2) \times 10^4\ m^{-2}$ over the upper 30 m (dry-weight biomass about 5 $g \cdot m^{-2}$). Most of this total is concentrated in the upper 5 m. Densities much greater than the average (exceeding 10 L^{-1}) occur around the outer margin of the Fraser River plume (Fig. 5; see also Parsons *et al.* 1969; Mackas and Louttit 1988). This species is an important food for herring and migrating juvenile salmon during its relatively brief period of peak abundance. In late May to early June, the population completes the feeding phase of its life history and migrates downward to "overwintering" depths exceeding 200 m. Harrison *et al.* (1983) suggested an annual secondary production of about 7 g C m^{-2} for this species alone. Despite its large contribution to the total zooplankton biomass and secondary productivity of the Strait of Georgia, there is little evidence that seabirds in the strait feed directly on *N. plumchrus*. The birds that have been shown to eat copepods locally (Cassin's Auklet [*Ptychoramphus aleuticus*] and the storm-petrels) do not inhabit the inner coast (Vermeer 1983). Phalaropes, which have been shown to be major copepod predators in other regions, are also much more common on the outer coast (K. Vermeer, pers. commun.). Although relatively large, *N. plumchrus* is only about half the length of its congener *N. cristatus* (the preferred food of the outer-coast Cassin's Auklet; Vermeer 1981; Vermeer *et al.* 1985) and may therefore be harder for birds to locate. Alternatively, *N. plumchrus* may be a highly suitable food, but the physical and biotic habitat of the Strait of Georgia may be too harsh (e.g., more predators, fewer nesting sites).

There is normally a large increase in the biomass of gelatinous zooplankton in June and July following the downward migration of *N. plumchrus*. Major taxonomic categories in the Strait of Georgia include medusae (*Phialidium, Aequorea, Aglantha*), ctenophores (*Pleurobrachia*), and appendicularians (*Oikopleura*). Other gelatinous plankton that occasionally reach high densities on the outer coast (salps, doliolids, and *Velella*) are extremely rare on the inner coast and probably occur only as vagrants. The larger gelatinous zooplankton should be available to seabirds. Both medusae and (at least in calm conditions) ctenophores are visually conspicuous and often abundant near the sea surface. Strandings along shorelines are also common. However, because of their high water and low organic content, their food value per unit wet weight is substantially lower than that of the crustacean zooplankton

Figure 2
Spatial distribution of euphausiid wet-weight biomass in the south and central Strait of Georgia: (A) 18–24 February 1981; (B) 30 March – 6 April 1981; (C) 11–15 May 1981; (D) 8–14 June 1981


A
B
C
D
125°
124°
123°
50°
49°
0 5 10 20
NAUTICAL MILES
0 5 10 20 30
KILOMETERS
VANCOUVER ISLAND
NANAIMO
VANCOUVER
CANADA
USA
SG-81-1 FEB 18-24, 1981
STOCK ESTIMATE 2.4 x 10³ T
SG-81-5 MARCH 30-APRIL 6, 1981
STOCK ESTIMATE 6.14 x 10³ T
SG-81-9 MAY 11-15, 1981
STOCK ESTIMATE 3.9 x 10³ T
SG-81-11 JUNE 8-14, 1981
STOCK ESTIMATE 5.5 x 10³ T
ABUNDANCE G/10m²
>30
10.1-30
5.1-10
0-5

or of most intertidal organisms. Their major importance to birds may be through their impact as predators on the total pelagic food web. Larson (1987) calculated that these organisms in Saanich Inlet can take 5–10% of surface-layer mesozooplankton biomass per day. Euphausiid eggs and larvae appear to be particularly vulnerable. Predation on larval fish is also thought to be significant in the Strait of Georgia (e.g., Arai and Hay 1982).

The remaining major component of the inner-coast zooplankton community consists of macrozooplankton. The important members of this group are the euphausiids, chaetognaths, amphipods, and larval fish. All are relatively large (5–25 mm), and many are strongly pigmented. The euphausiids and amphipods are the only plankton groups known to be used as food by seabirds in the Strait of Georgia (Vermeer *et al.* 1987). Most species spend daylight hours below the surface layer and are available to surface-feeding birds only when they migrate (more or less routinely) to the surface at night or where and when special circumstances cause swarming at the sea surface. Both of these situations will be discussed in greater detail later in the paper.

The major euphausiid species reported from the Strait of Georgia include *Euphausia pacifica, Thysanoessa spinifera, T. longipes* (perhaps confused with *T. inspinata*), and *T. raschii*. All are about 15–25 mm in length as late juveniles and adults. Heath (1977) used night surface net tows to examine the seasonal cycle of standing stock and

Figure 3
Time series of total euphausiid stock size, February–June 1981. Trend line is our subjective interpretation of the probable seasonal growth-minus-mortality curve for the south and central Strait of Georgia population. Isolated high value in April probably represents a brief advection of animals into and out of the sampled region.

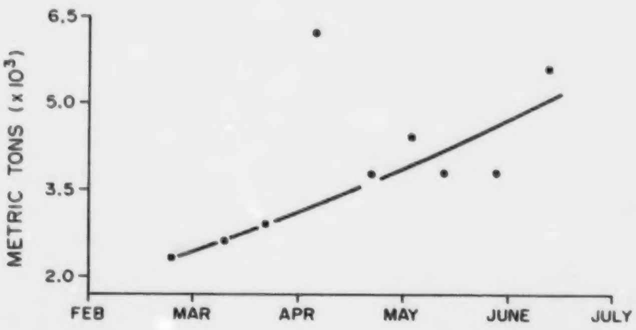
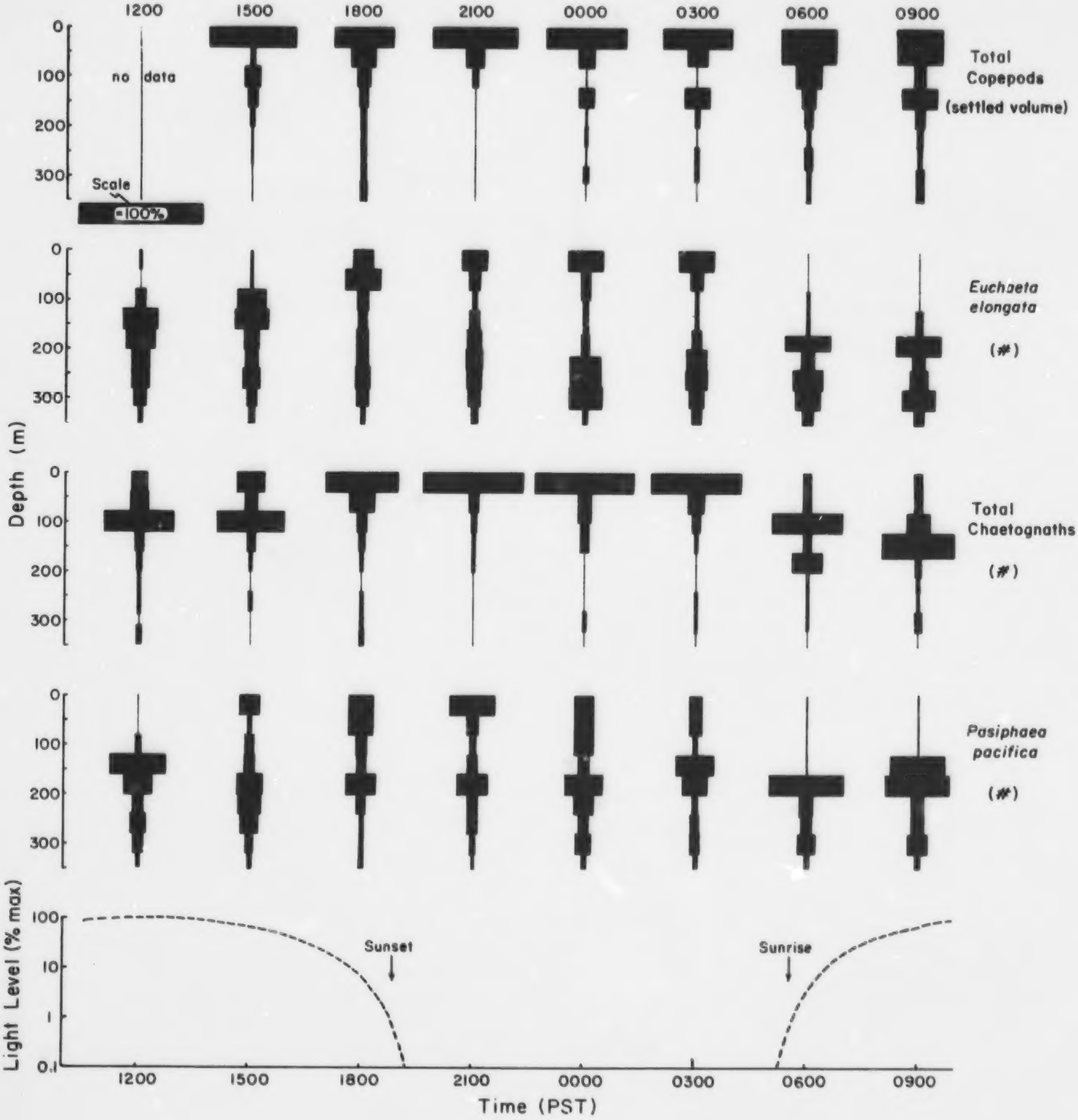
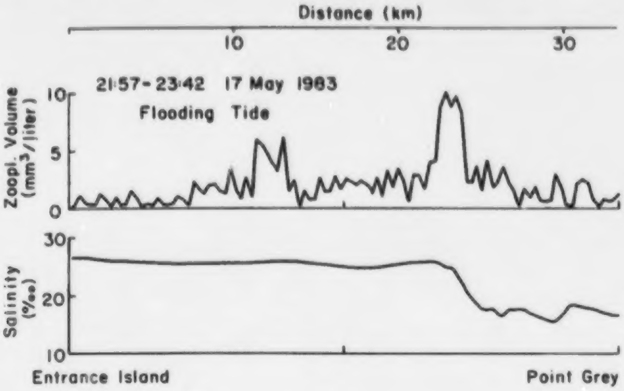


Figure 4
Vertical distribution of selected zooplankton taxa over a day-night cycle. Data are plotted as percentage of total water-column population found in each depth stratum.



productivity for inner-coast populations of *E. pacifica*. Highest concentrations of euphausiids occur in inlets and reach about five times the average for the open strait. Harrison *et al.* (1983) estimated from Heath's (1977) data that euphausiid secondary production is about 10–20% of copepod secondary production, and that biomass in the surface layer is at its maximum in October–December (dry weight about 0.1 $g \cdot m^{-3}$) and minimum in March–May (about 0.015 $g \cdot m^{-3}$). Estimates of vertically integrated euphausiid biomass were obtained for the southeast half of the Strait of Georgia during February–June 1981 (J.C. Mason and J. Fulton, unpubl. data). Figures 2A–D show representative maps. Within each survey, densities were found to vary from place to place by a factor of 50 or more. There appeared to be no consistently preferred patch locations, possibly due to seasonal relocation of the population. Stations located off the passes between the Gulf Islands showed especially strong time variability, with both

Figure 5
Aggregation of the copepod *Neocalanus plumchrus* at the frontal margin of the Fraser River plume. Data were obtained at 1-min intervals from a research vessel steaming at 15 $km \cdot h^{-1}$. Upper panel shows copepod biomass measured as particle volume (*N. plumchrus* copepodites are about 1 mm^3 per individual). Lower panel shows salinity.



extremely high (cruise SG-81-9) and extremely low (cruise SG-81-5) population densities occurring in the same locations. Figure 3 shows, for the same data, the time series of total biomass summed over the mapped region. With the exception of one high value in April (probably caused by advection from outside the sampled region, as most of the high values in April were at the northwest margin of the study area), there was a steady increase from February through to mid-June, inconsistent with the seasonal pattern of winter maximum and early summer minimum described by Heath (1977) and Harrison *et al.* (1983). We believe the data shown in Figures 2 and 3 are more representative. The discrepancy in seasonal pattern is probably due to differences in sampling methodology; Heath (1977) used surface horizontal tows, whereas the 1981 surveys used vertically integrated oblique tows. Heath's (1977) results would therefore be strongly affected by seasonal changes in the range and intensity of vertical migration.

We know of no published information on the horizontal distribution and productivity of chaetognaths and planktonic amphipods on the inner coast. Their vertical distribution (especially in Saanich Inlet) has been discussed by Mackie and Mills (1983) and Mackie (1985). Important amphipod taxa include *Cyphocaris challengeri* and *Parathemisto pacifica*. The dominant chaetognath is *Sagitta elegans*.

6. Small- to mesoscale spatial heterogeneity of Strait of Georgia zooplankton populations

Patchiness in plankton abundance occurs over a broad range of spatial scales and is generated by a variety of physical and biological processes, such as advection, growth, predation, competition, and behaviour (Haury *et al.* 1978; Mackas *et al.* 1985). Large patches tend to grow and decay slowly, whereas small ones form and decay quickly. Large-scale pattern (tens to hundreds of kilometres) is primarily caused by slow and sustained processes, such as mean advection, population growth, predation, and competition. Small-scale pattern (tens to hundreds of metres) is produced by more rapid and transitory physical and biological mechanisms, such as frontal accumulation and migration. Although predation is unlikely to form small-scale patches, it may be important in limiting their intensity and persistence.

In general, large animals can swim faster and for a longer time in a given direction and thus are more able to form patches. However, they also mature more slowly and have lower intrinsic rates of population increase. For the larger zooplankton likely to be of greatest importance to seabirds, the small-scale spatial variability observed within the Strait of Georgia must be due either directly to behaviour (e.g., migration and swarming) or to interaction of behaviour with small-scale physical processes (e.g., vertical swimming interacting with horizontal convergence and divergence). In the remainder of this section, we discuss a few situations in which these processes appear to affect strongly the distribution and availability of zooplankton.

6.1. Diel vertical migration

Many pelagic organisms move closer to the sea surface at night and to greater depths in daylight. Zooplankton typically move tens to hundreds of metres up and down. The most plausible explanation for this behaviour is that it reduces risk of capture by visual predators. For the aspiring predator, the converse is true—a meal is hard to acquire near the surface in daylight because the prey are absent and at night because the prey cannot be detected in the prevailing gloom.

Within the Strait of Georgia ecosystem, the intensity of the diel migration varies among the zooplankton. In general, migration is strongest for large and/or strongly pigmented organisms. Figure 4 shows time series of vertical distributions collected in mid-strait in April 1983 by J. Mason and A. Phillips and analyzed by J. Fulton and O. Kennedy. Herbivorous copepods (primarily copepodites of *N. plumchrus*) are most abundant in the upper 20 m in all sampling periods. In contrast, large organisms, such as the carnivorous copepod *Euchaeta elongata*, chaetognaths (primarily *Sagitta elegans*), and the glass shrimp *Pasiphaea pacifica*, show strong vertical migration. The timing of their upward and downward movement is phase-shifted ahead of the day–night cycle by several hours. The migratory species reach nearly the upward extreme of their migration by 18:00 or 21:00 but have already moved down to their daytime depth by 06:00. This implies that crepuscular (dawn- and dusk-active) planktivores should feed more successfully at dusk than at dawn.

6.2. Surface swarming by macrozooplankton

Examples of surface swarming events in local waters are noted in Table 1. Vermeer *et al.* (1987) observed active feeding by Mew Gulls (*Larus canus*) and Bonaparte's Gulls (*L. philadelphia*) on dense swarms of euphausiids and hyperiid amphipods in Active Pass. Swarms occurred predictably at this location and were correlated in both time and space with upwelling produced by vertical deflection of strong tidal flows as they encountered steeply sloping bathymetry (essentially the same mechanism proposed by Brown *et al.* [1979] and Braune and Gaskin [1982]). A similar rapid upwelling has been implicated in occasional mass mortality of hake in the same region (Herlinveaux *et al.* 1986): the fish are moved upward so rapidly that they are unable to control the expansion of their swim bladder, and they arrive at the surface bloated and immobilized and fall victim to waiting predators, such as gulls and eagles.

Beach strandings of euphausiids, perhaps related to surface swarming, have been reported occasionally from the Strait of Georgia (Table 2). These reports are often by members of the public concerned about the possibility of pollution killing "baby shrimp" (M. Waldichuk, pers.

Table 1
Observations of daytime surface swarming of euphausiids, made by staff at the Pacific Biological Station

Date	Observer	Location	Remarks
6 April 1965	P. Wickett	5 km WSW of Lasqueti Island	*Euphausia pacifica* observed in daylight surface shoals. No estimate of concentration.
19 November 1980	D. Miller	Approximately 2 km south of Porlier Pass	Dense schools of *Euphausia pacifica* above a large school of herring. Mean body length 13.34 mm. Euphausiids were clumped into tightly packed "balls" about 2–3 m in diameter with narrow columns or strings of euphausiids streaming between clumps. Herring and birds appeared to be actively feeding all day long. Concentration within swarms estimated at 16 $g \cdot L^{-1}$ (about 6×10^5 animals m^{-3}) by weighing a sample taken with a small dip net.
11 March 1986	J. Fulton	Departure Bay, Nanaimo	First noticed because of surface-feeding activity of Bonaparte's Gulls. Euphausiids in oval swarms about 1 m × 2 m × 5 cm, with the distance between adjoining swarms varying between 3 and 10 m. Concentrations estimated at 1.9×10^3 m^{-3} by observation of the distances between organisms (Mackie and Mills 1983).

Table 2
Reports of euphausiids stranded on beaches

Date	Location	Tide	Moon	Sky	Wind	Remarks
29 May 1966	Rebecca Spit, Quadra Island	High 4.2 m at 00:32; low 2.1 m at 07:30	First quarter 27 May	Overcast with rain	SE breezes	Estimated by a Department of Agriculture inspector as 6000 kg in several rows, seaward of the high-tide line and extending along the beach for 4 km. Remarkable bird activity—"birds too full to fly." No sample collected but described as looking like "baby shrimp."
2 April 1970	Gabriola Island ferry dock	High 4.3 m at 03:10; low 2.8 m at 09:00	New moon 4 April	Overcast with rain	-	Sample taken by ferry captain who observed very actively feeding birds. The sample was 90% *Euphausia pacifica*, 9% crab zoea (*Cancer magister*), and traces of gamariid amphipods.
8 May 1980	Hornby Island ferry dock	High 4.1 m at 23:58; low 3.2 m at 05:48	Last quarter	Overcast	-	Sample taken by ferry captain contained mostly *Euphausia pacifica*, with traces of *Thysanoessa spinifera* and zoea of *Cancer magister*. The euphausiids were in breeding condition. Over 20% of the female *E. pacifica* had spermathecae attached. Although *Thysanoessa longipes* made up 30% of euphausiid biomass in plankton samples collected downwind of Hornby Island 10 d earlier, none was found stranded.

commun.). The instances described in the table had in common dark nights with high tides before dawn, onshore winds (not storms), and bird populations feeding to satiation.

6.3. Aggregation of zooplankton at convergent fronts

Copepod aggregations at the outer margin of the Fraser River plume have been studied recently by Mackas and Louttit (1988). The sharpness of the horizontal salinity gradient at the plume boundary is maintained by surface convergence of plume and higher-salinity water. Near-surface abundances of copepods at the plume edge average about 10^4 m^{-3} and range up to nearly 10^5 m^{-3} (Fig. 5). This can represent a concentration factor of several hundred-fold over background population densities elsewhere in the Strait of Georgia; at the plume edge, two to three times as many animals can be crowded into a single cubic metre of water as are normally spread over an entire 200- to 300-m water column. Mackas and Louttit (1988) showed that these dense plume-edge aggregations form and disperse within a few hours to a few days, far more rapidly than can be accounted for by growth or mortality rates. The plume in the Strait of Georgia is a 2- to 10-m-thick lens of brackish surface water that slides with only a minimum of resistance over the underlying denser and more saline water. The plume appears to accumulate and retain high densities of organisms at its outer margin whenever (because of tides, southeast winds, or increasing river discharge) it advances outward. Conversely, the animals are shed back into the water column whenever physical processes cause the plume to recede. Directed horizontal swimming by the copepods is too slow to track the observed frontal displacements. The only plausible mechanism is an interaction of vertical swimming with water movement at the frontal boundary of the plume (where swimming upward would trap animals in the oblique downdraft from a surface convergence).

6.4. Patches associated with near-surface internal waves

Convergent water motions produced by internal waves provide another process for aggregation and transport of plankton. Like surface gravity waves (sea and swell), internal gravity waves are vertical undulations of a density gradient. For internal waves, this density gradient is provided by the internal stratification of the water column rather than by the air–water density contrast across the sea surface (see Thomson 1981, for a good introduction). Compared with those of surface waves, propagation speeds of internal waves are slow (typically about 0.5 $m \cdot s^{-1}$ in the Strait of Georgia), but vertical amplitudes are large (5–10 m or more). Because of the strong vertical stratification and high current shears occurring in many inner-coast waters, internal waves are widespread and important in the physical oceanographic environment (LeBlond 1983).

Animals seeking to maintain a fixed depth by vertical swimming can find themselves trapped at a fixed location relative to the horizontally moving internal wave crest. The wave transports the animals already "riding" the waveform and picks up additional passengers as it propagates through the water (for examples and more detailed explanations, see Zeldis and Jillett 1982; Shanks 1985). There are several locations on the BC inner coast where internal wave patterns are strong and highly directional. However, their importance in controlling plankton distributions has not yet been evaluated.

7. Summary

The zooplankton occupy important positions in the food web of the Strait of Georgia. However, relatively few of the marine birds found in the strait are obligate planktivores. Observed instances of planktivory suggest that it is locally an opportunistic phenomenon associated with shoreline stranding or surface swarming of large-bodied zooplankton. Behavioural activity of the zooplankton and interactions of this behaviour with near-surface water movement are important in generating localized dense patches of zooplankton, which in turn provide regions of high prey availability for marine birds.

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Molluscan fisheries and marine birds in the Strait of Georgia

Neil Bourne

1. Abstract

Molluscan resources in British Columbia support valuable commercial fisheries and are used widely in the recreational fishery. In 1986, the landed weight of molluscs in commercial fisheries was 12 939 t, with a value of $11.9 million. Many of these fisheries are in the Strait of Georgia, which is also an important wintering area for marine birds. A brief overview of the distribution, biology, and harvesting of molluscs in commercial fisheries in the Strait of Georgia is presented, and conflicts with marine birds are identified. Only minor fisheries for cephalopods—octopus and squid—occur in the Strait of Georgia. Eleven species of bivalves are harvested in commercial intertidal and subtidal fisheries in the strait, and most species are also used in the recreational fishery. Predation by marine birds, particularly ducks, on bivalves has been reported in several areas of the Strait of Georgia, and this predation can be important in areas where bivalve culture is practised.

2. Résumé

En Colombie-Britannique, il existe d'importantes pêcheries commerciales de mollusques, et la pêche sportive de ces espèces est également largement répandue. En 1986, les pêcheries commerciales ont permis de récolter des mollusques dont le poids à l'embarquement était de 12 939 t, et la valeur, de 11,9 millions de dollars. Nombre de ces pêcheries se trouvent dans le détroit de Georgia, qui est également une importante aire d'hivernage pour les oiseaux marins. L'auteur présente un bref aperçu de la distribution, de la biologie et de la récolte des mollusques à des fins commerciales dans le détroit de Georgia et indique les conflits qui existent avec les oiseaux marins. Il y a seulement quelques pêcheries peu importantes de Céphalopodes—pieuvres et calmars—dans le détroit de Georgia. Onze espèces de bivalves sont récoltées dans les pêcheries intertidales et infralittorales du détroit, et la plupart des espèces sont également pêchées à des fins sportives. On a signalé que, à plusieurs endroits du détroit de Georgia, les oiseaux marins, notamment les canards, s'attaquaient aux bivalves, et cette prédation peut être importante là où on fait la culture de ces mollusques.

3. Introduction

Coastal waters in British Columbia have a rich molluscan fauna. Bernard (1970) estimated that there were 517 species of marine molluscs, which included representatives from the five classes in the phylum Mollusca: 29 Polyplacophora; 283 Gastropoda; 180 Bivalvia; 5 Scaphopoda; and 21 Cephalopoda. The exact number of marine molluscs occurring in the Strait of Georgia is unknown, but it is believed that over 60% of species occurring along the coast are found there (F.R. Bernard, pers. commun.).

Molluscan resources in British Columbia support valuable commercial fisheries (Quayle 1969*b*, 1988; Quayle and Bourne 1972; Ketchen *et al.* 1983; Jamieson and Francis 1986). Although more than 500 species of molluscs occur along the coast, less than 20 are utilized in commercial fisheries. In 1986, total landed weight of commercial molluscs in British Columbia was 12 939 t, with a value of about $11.9 million (Table 1). These landings are not large when compared with total fishery landings for the coast, but molluscan fisheries are valuable to the economic life of many coastal communities. Further, molluscan resources

Table 1
Landings of inshore molluscs in British Columbia, 1984–86

Species	Parameter[a]	1986	1985	1984
Bivalves				
Intertidal clams	Weight	2 848.7	2 926.1	2 614.5
	Value	3 741.0	3 287.7	2 756.8
Oysters	Weight	4 734.0	3 420.0	3 542.0
	Value	2 563.0	2 600.0	2 000.0
Geoducks	Weight	5 005.6	5 166.7	3 842.9
	Value	4 294.0	4 605.1	2 937.0
Horse clams	Weight	94.0	6.3	6.7
	Value	62.0	5.9	5.0
Scallops	Weight	71.1	53.4	17.9
	Value	227.0	135.0	74.0
Mussels	Weight	2.2	–	–
	Value	4.0	–	–
Gastropods				
Abalone	Weight	51.5	42.2	57.9
	Value	734.0	441.7	530.0
Cephalopods				
Octopus	Weight	53.1	34.1	25.0
	Value	136.0	81.8	56.0
Squid	Weight	78.6	111.3	13.7
	Value	127.0	185.5	17.4
Total	**Weight**	**12 938.8**	**11 760.1**	**10 120.6**
	Value	**11 888.0**	**11 342.7**	**8 376.2**

[a] Weight in tonnes, value in thousands of Canadian dollars.

are used extensively in the recreational fishery (Carmichael and Bourne 1986; Bourne *et al.* 1987).

This paper examines the relationship between marine birds and molluscs of commercial importance in the Strait of Georgia area of British Columbia. Only molluscs in the classes Cephalopoda, Gastropoda, and Bivalvia are considered. Emphasis is on bivalves because they support the largest commercial molluscan fisheries along the coast and in the Strait of Georgia and are also important in diets of marine birds.

The Strait of Georgia as defined here extends from the Discovery Passage - Yuculta Rapids area in the north and south to the tip of Saanich Peninsula and eastward to the international border, including Boundary Bay. This includes Department of Fisheries and Oceans Statistical Areas 13–18 inclusive and Areas 28 and 29 (Fig. 1). The northern half of Area 13 lies outside this definition of the Strait of Georgia, but fisheries statistics are reported only for the entire area.

4. Cephalopoda

The class Cephalopoda includes octopus and squid; these molluscs—particularly squid—can form an important part of the diet of many marine birds (Nelson 1979; Schneider and Hunt 1984; Hatch 1984).

4.1. Octopus

Three species of octopus have been recorded in the shallow coastal waters of British Columbia, and all occur in the Strait of Georgia: giant Pacific octopus (*Octopus dofleini*) and two small species, *O. rubescens* and *O. leioderma* (Jamieson and Francis 1986). The large *O. dofleini* is the only species exploited commercially.

The giant Pacific octopus occurs throughout BC coastal waters and is common in the Strait of Georgia, but no estimates of population size have been made for this area. Larvae that hatch from eggs suspended in strands within a den are about 7 mm in length and are planktonic in the upper water layers for about two months before settling to the bottom in inshore waters (Hartwick 1973). Growth is rapid—males mature at about 12 kg after 18 months but may grow to over 25 kg. Females mature at about 20 kg. The life span of both sexes is about 3–5 yr (Hartwick *et al.* 1981; Jamieson and Francis 1986).

The fishery for octopus in British Columbia is small, and landings in the last 3 yr have been under 55 t (Table 1). Most of the catch is a by-catch in shrimp and groundfish trawling outside the Strait of Georgia. Attempts have been made to harvest octopus commercially with traps similar to those used in Japan (Mottet 1975), but they have not been successful (Jamieson and Francis 1986). Recently, landings have been made by scuba divers in the strait (R. Harbo, pers. commun.). Octopus caught in the commercial fishery are used mostly for bait in the groundfish fishery, but some are used for human consumption.

The octopus resource is probably underutilized, and the fishery could be expanded (Jamieson and Francis 1986). Landings may increase in the future, particularly if a larger part of the catch is used for human consumption, but it is not expected that it will become a major fishery in the strait.

Octopus are eaten by seabirds (Hatch 1984) but are probably of minor importance in the diet of marine birds in the Strait of Georgia. Adult octopus are nocturnal and secretive, and their large size probably makes them unacceptable as food for marine birds. Planktonic larvae or early juveniles and the two smaller species may be of some importance in the diet of some marine birds, but there is no information on this.

4.2. Squid

Squid probably form a significant part of the biomass in the northeast Pacific Ocean and have a major trophic role in the Strait of Georgia (Jefferts 1986; F.R. Bernard, pers. commun.). Seventeen species are known to occur in BC waters, but only four appear to have commercial potential: opal (*Loligo opalescens*); red (*Berryteuthis magister*); nail (*Onychoteuthis borealijaponica*); and flying (*Ommastrephes bartrami*) (Bernard 1980; Heritage 1986). Of these four species, only the opal and red squid occur in the strait (Bernard 1980).

Opal squid occur from the Gulf of Alaska to central Baja California (Fields 1965; Heritage 1986). They are common in the Strait of Georgia and are frequently seen at night in well-illuminated inshore areas, but there are no estimates of population size. Spawning can occur throughout the year, but the peak period is between February and August. Recently hatched opal squid are planktonic in the surface waters. Growth is rapid, and, when they attain a mantle length of about 4 cm, they move closer to the bottom. At a mantle length of about 8 cm, they begin to school with other individuals. Sexual maturity can be attained after 1 yr, and the total life span is estimated to be less than 2 yr.

Red squid occur from Monterey, California, to the Bering Sea. They appear to spend most of their lives on or near the bottom but will rise to the surface and at times are attracted to artificial light (Bernard 1980). Red squid may be present in reasonable numbers in the Strait of Georgia, but little is known about the biology of this species.

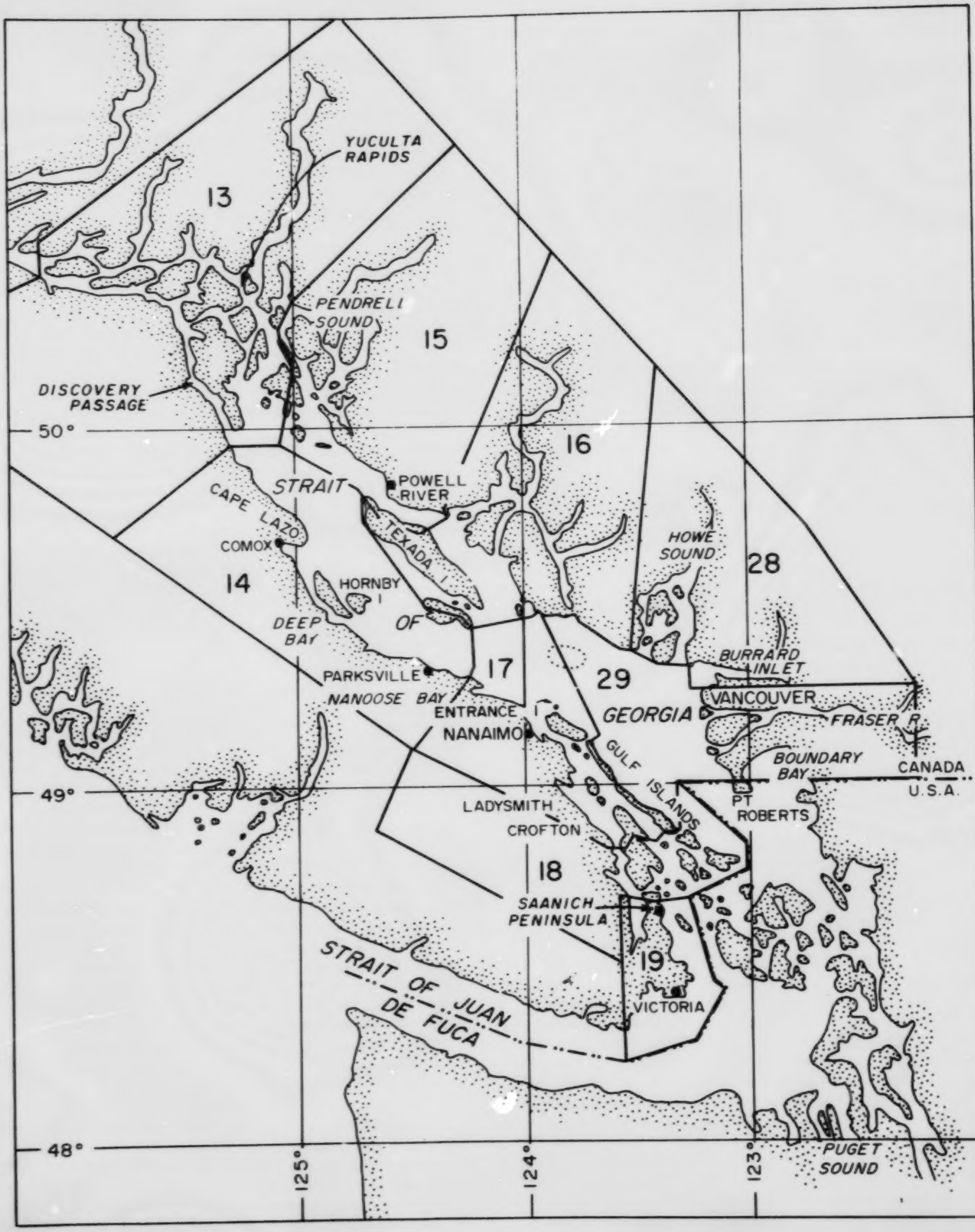
Most of the inshore BC squid catch is a by-catch in otter trawling for shrimp and groundfish. A major fishery for opal squid occurs off California (Fields 1965), and attempts have been made to harvest this species in British Columbia, including the Strait of Georgia, although most of the effort has been on the west coast of Vancouver Island (G.D. Heritage, pers. commun.). Fishing is at night. Bright lights are used to attract schools of spawning squid, which are captured with seines. The major factor against development of a sizeable commercial fishery is the extended breeding season and erratic occurrence of spawning schools (Bernard 1980). It is impossible to predict when and where schools will occur, which makes the fishery unprofitable.

Squid are an important item in the diet of many marine birds (Nelson 1979; Schneider and Hunt 1984) but are not known to be an important food item of marine birds in the Strait of Georgia. Establishment of a large squid fishery in the strait does not appear likely, and no conflicts between a squid fishery and marine bird populations there are foreseen.

5. Gastropods

Most molluscan species in BC coastal waters are gastropods (Bernard 1970), and many species occur in the Strait of Georgia in a variety of habitats. Only one species, the northern abalone (*Haliotis kamtschatkana*), is harvested commercially. Occasionally minor landings of "snails" are reported in the statistics. These are small experimental fisheries usually for top-shells or turban shells, *Tegula* sp.,

Figure 1
Map of the Strait of Georgia area, British Columbia, showing the Department of Fisheries and Oceans statistical areas


YUCULTA RAPIDS
13
PENDRELL SOUND
15
DISCOVERY PASSAGE
50°
16
STRAIT
POWELL RIVER
CAPE LAZO
COMOX
TEXADA I
HOWE SOUND
28
14
HORNBY I
DEEP BAY
OF
17
29
BURRARD INLET
PARKSVILLE
NANOOSE BAY
ENTRANCE I
VANCOUVER
GEORGIA
FRASER R.
NANAIMO
GULF ISLANDS
BOUNDARY BAY
CANADA
U.S.A.
49°
LADYSMITH
PT ROBERTS
CROFTON
18
SAANICH PENINSULA
19
VICTORIA
STRAIT OF JUAN DE FUCA
48°
125°
124°
123°
PUGET SOUND

and *Astraea gibberosa*, and landings are from more oceanic locations.

The northern abalone occurs from northern Mexico to Alaska (Jamieson and Francis 1986). In British Columbia, it occurs from the lower part of the intertidal zone to subtidal depths of about 15 m. Distribution is patchy, but most of the population occurs on the outer coast. Abalone were not recorded in the Strait of Georgia until the early 1950s (D.B. Quayle, pers. commun.). They are not common in the strait, and all populations are subtidal.

Gastropods may be carnivorous or herbivorous (Griffith 1967). Species in families such as Naticidae and Muricidae feed on other molluscs, ascidians, and barnacles and may prey on bivalves of commercial importance. Other gastropods, such as those in the families Acmaeidae, Haliotidae, Trochidae, and Littorinidae, are herbivores and feed by scraping surface algae and other plants off substrates. Detritus may be of importance to some gastropods.

Growth rates have not been determined for most species of gastropods in British Columbia. Growth of abalone is slow, 6–10 yr being required to attain a shell length of 100 mm, the minimum legal size limit in the commercial fishery (Breen 1986).

A few studies have determined gastropod abundance in local areas (e.g., moonsnails [Bernard 1967]; Japanese oyster drills [D.B. Quayle, pers. commun.]), but there are no estimates of abundance of any gastropod species in the Strait of Georgia. Attempts have been made to estimate abalone populations in the northern area of British Columbia (Breen 1986), and mean densities ranging from 0.65 to 2.53 per square metre were reported.

The commercial fishery for abalone is on subtidal stock, and harvest is by divers equipped with either scuba or hookah gear. In recent years, landings have been under 60 t (Table 1) because of reduced stocks, license limitation, and quotas on commercial harvest. Most of the fishery is in the northern area, but some landings have been from the west coast of Vancouver Island. Previously, occasional commercial landings of abalone were made in the Strait of Georgia, but the area is now closed to commercial fishing.

Abalone are harvested in the recreational fishery, including in the Strait of Georgia, but the amount landed is unknown (Carmichael and Bourne 1986). The recreational catch is regulated by a daily limit. Other species of gastropods may be harvested in the recreational fishery for food, curios, or souvenirs, but the amount taken is minor.

Gastropods are eaten by many marine birds and form a significant part of their diet in the Strait of Georgia (Vermeer 1982*a*, 1983; Vermeer and Bourne 1984; Bourne 1984). Sixteen species of gastropods were identified in the gut contents of Buffleheads (*Bucephala albeola*) and Barrow's Goldeneyes (*B. islandica*), 21 in Harlequin Ducks (*Histrionicus histrionicus*), and 18 in White-winged Scoters (*Melanitta deglandi*) in the strait (Vermeer 1982*a*, 1983; Vermeer and Bourne 1984). All gastropod species were small and of no importance in commercial fisheries. Cormorants, *Phalacrocorax* sp., have been suspected as being possible predators of abalone in the strait (D.B. Quayle, pers. commun.), and abalone are eaten by Glaucous-winged Gulls (*Larus glaucescens*) (Vermeer 1982*b*). However, it is doubtful if marine birds are significant predators on abalone in the strait or elsewhere. Adult abalone are generally found firmly attached to rocks, often hidden in rock crevices, and it is unlikely that marine birds could pry adults off rocks.

6. Bivalves

Many of the 180 species of bivalves reported from BC coastal waters occur in the Strait of Georgia. Bivalves are the most important class of molluscs in commercial fisheries of British Columbia (Table 1). In 1966, 98.6% of the weight and 91.5% of the landed value of commercial molluscan fisheries in British Columbia were bivalves. The major fisheries are for intertidal clams: razor (*Siliqua patula*); butter (*Saxidomus giganteus*); littleneck (*Protothaca staminea*); manila (*Tapes philippinarum*); and a category termed mixed clams, which is usually a mixture of littleneck and manila clams, although it may also contain minor landings of cockles (*Clinocardium nuttallii*) and soft-shell clams (*Mya arenaria*) (Fig. 2). Three species of clams are harvested in subtidal fisheries—geoducks (*Panope abrupta*) and two species of horse clams, *Tresus capax* and *T. nuttallii* (Fig. 3). One species of oyster, the Pacific oyster (*Crassostrea gigas*), supports a valuable industry (Fig. 4). Small quantities of blue mussels (*Mytilus edulis*) and two species of scallops, pink (*Chlamys rubida*) and spiny (*C. hastata*), are also landed (Table 1).

Razor clams are found only on ocean-swept sand beaches and do not occur in the Strait of Georgia, but the other three species of intertidal clams are common on many beaches there (Quayle and Bourne 1972). Butter clams occur from the Aleutian Islands to California. In the strait, they are found mainly in the lower third of the intertidal zone to subtidal depths of 10 m, mostly in sand-broken shell–mud–gravel substrates. Littleneck clams occur from lower California to the Aleutian Islands. In the strait, they are most abundant from about the mid-intertidal beach to the 1-m tidal level but are found to subtidal depths of 12 m. They occur with butter clams but are more common in firmer substrates. The manila clam is an exotic that was accidentally imported into British Columbia along with Pacific oyster seed from Japan (Bourne 1978). It spread quickly throughout the strait, along the west coast of Vancouver Island; recently it has spread across Queen Charlotte Sound and now occurs as far north as Bella Bella (Bourne 1982). Manila clams occur from the 1-m intertidal level to well above the mid-intertidal area, generally on sand–gravel beaches. No subtidal populations are known in British Columbia.

Geoducks occur from Alaska to California from the lower intertidal zone to subtidal depths of at least 120 m (Bernard 1983). They occur throughout British Columbia in moderately exposed to sheltered conditions in fine mud to sand–gravel substrates. The two species of horse clams are also widely dispersed. *Tresus capax* occurs from Alaska to California, whereas *T. nuttallii* has a slightly more restricted distribution. They occur in the lower third of the intertidal zone to subtidal depths of 10 m. *Tresus capax* occurs mostly in mud–sand–gravel substrates, whereas *T. nuttallii* occurs in sand substrates. All three species are common in the Strait of Georgia.

Three species of oysters have been harvested commercially in British Columbia: native (*Ostrea lurida*); eastern (*Crassostrea virginica*); and Pacific (*C. gigas*) (Quayle 1969*b*, 1988). Native oysters occur from lower California to Alaska, well down in the intertidal zone. They have a discontinuous distribution in the Strait of Georgia and occur mostly in sloughs and tidal lagoons. They were harvested in wild fisheries until about 1930 but are not used now commercially. Eastern oysters were imported into Boundary Bay from about the turn of the century to 1940.

Figure 2
Landings of clams in intertidal fisheries, 1951–86: (A) total landings for British Columbia; (B) landings for the Strait of Georgia

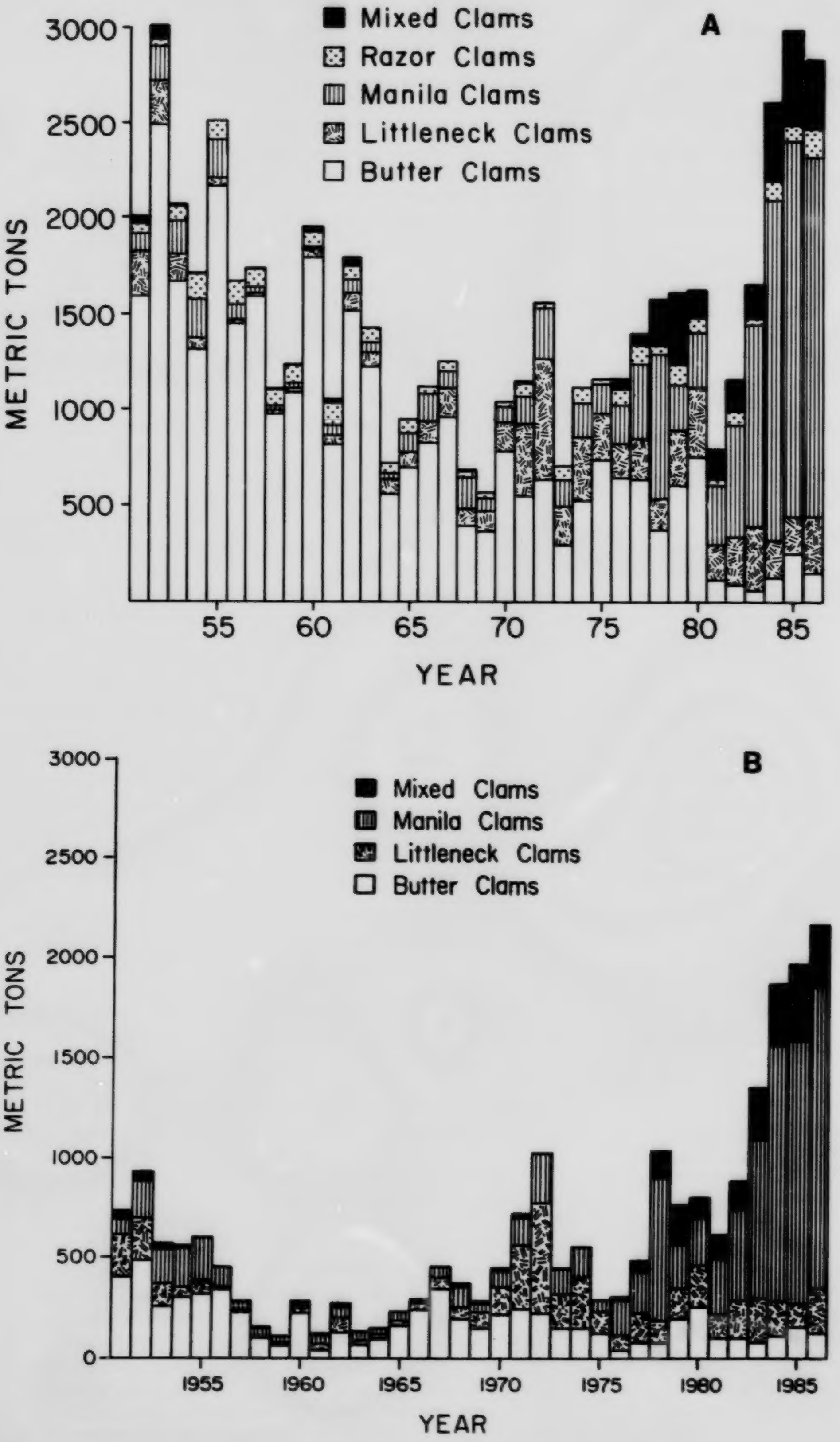
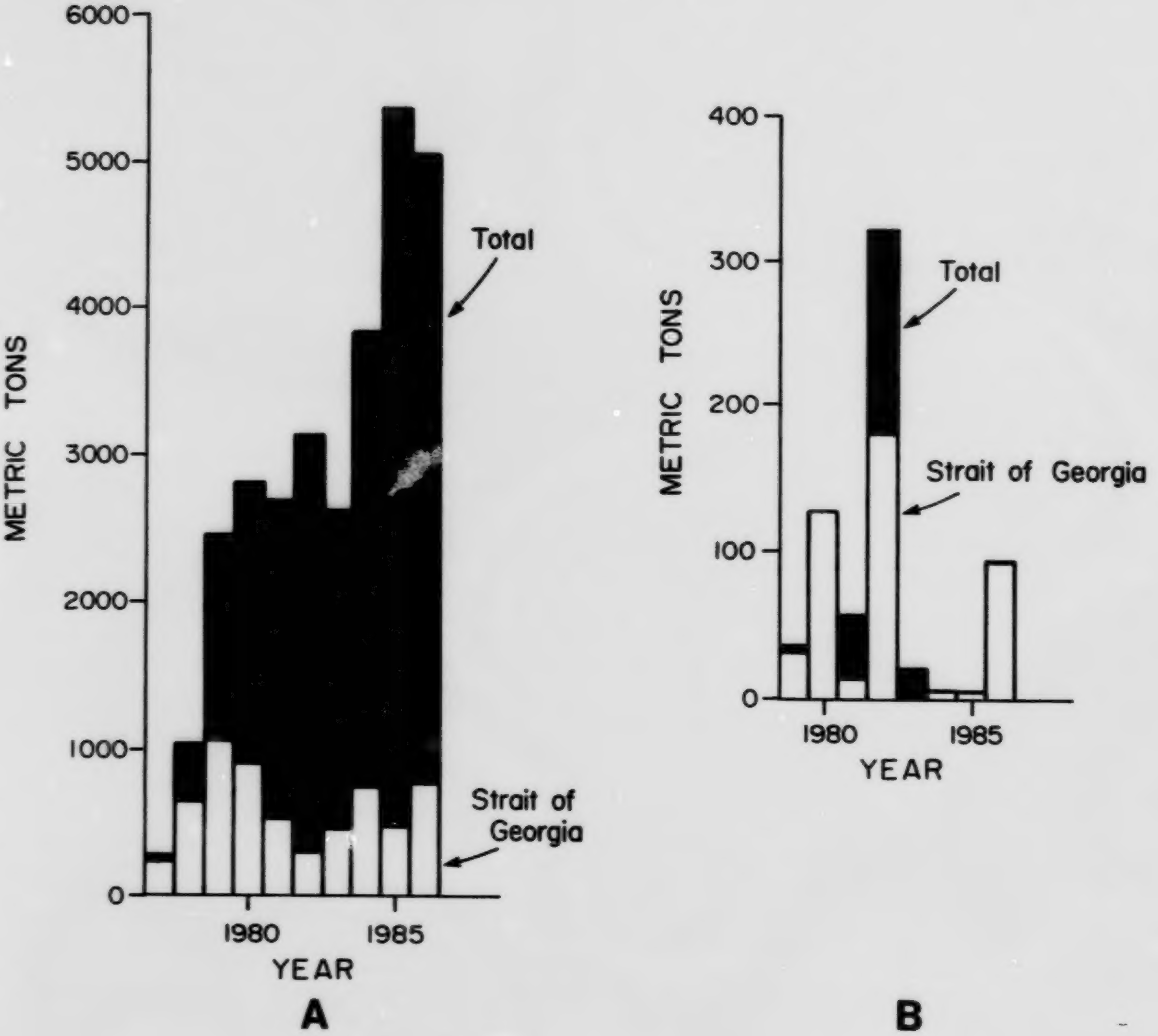


Figure 3
Landings of clams in subtidal fisheries, 1976–86: (A) geoducks; (B) horse clams



A small noncommercial relic population remains there. Pacific oysters were imported from Japan in 1912, and numerous importations of juveniles were made subsequently until about 1970 (Quayle 1969*b*; Bourne 1978). It is the only commercial species now in British Columbia, and the industry is centred in the strait.

Blue mussels are circumboreal and ubiquitous throughout coastal British Columbia in a wide variety of habitats (Bernard 1983). They generally occur in the upper half of the intertidal area and are common in the Strait of Georgia.

Thirteen species of scallops occur in BC coastal waters, but only two are harvested commercially—pink and spiny (Bourne 1969; Bernard 1983). Both species are found from California to Alaska. Pink scallops occur subtidally from 5 to 200 m mostly on mud bottom, and spiny scallops are found between 5 and 150 m on rocky bottom in areas of strong current. Both species occur throughout British Columbia, including the Strait of Georgia, although distribution is discontinuous.

Growth of most bivalves in British Columbia is slow and varies with species and environmental conditions. Butter clams reach the legal size in commercial fisheries (63-mm shell length) in 5–6 yr in the Strait of Georgia, 6.5–8.5 yr in the Alert Bay area, and 9 yr in the Prince Rupert area (Quayle and Bourne 1972). Manila and littleneck clams reach the legal size in the commercial fishery (38-mm shell length) in 3.5–4 yr in the strait. Manila and littleneck clams rarely live longer than 8 yr and butter clams 20 yr, but geoducks have been aged at over 150 yr.

Estimating populations of bivalves for extensive areas such as the Strait of Georgia is difficult. There are numerous beaches in the strait, and intertidal clams can vary considerably in growth, mortality, recruitment, and population structure from beach to beach. Estimates of clam populations have been made for a few individual beaches in the strait (e.g., Seal Island and Savary Island; Quayle and Bourne 1972; Bourne and Adkins 1985), but there is no general estimate of population for the entire area. No estimates have been made of subtidal bivalve populations in the strait except in limited study areas.

A major problem in bivalve fisheries in British Columbia is the occurrence of PSP (paralytic shellfish poisoning) or red tide (Quayle 1969*a*). This occurs when a microscopic one-celled organism, ***Protogonyaulax catenella*** or *P. acatenella*, increases rapidly to cause bloom conditions. These two organisms contain a highly toxic material. The organisms are ingested by bivalves; although the bivalves do not appear to be affected themselves, they become toxic to warm-blooded animals. The entire north coast of British Columbia has been closed to the harvest of intertidal clams since 1963 because of low levels of PSP, and there is a seasonal closure on the west coast of Vancouver Island for the same reason. Although PSP is not a major problem in the Strait of Georgia, there have been periodic closures of some local areas, and on occasion the entire strait has been closed to the taking of bivalves.

A fishery for intertidal clams began before the turn of the century and has continued to the present (Quayle and Bourne 1972). Little equipment is required—some means of getting to a clam beach, a fork or rake to dig clams, and a sack or basket to hold them. For many years, the most important species in the fishery was the butter clam, which was usually canned (Fig. 2). This continued until the mid-1970s, when the market switched from butter to steamer clams, i.e., littleneck and manila clams. Production of butter clams has declined since then because of PSP and pollution closures, socioeconomic factors, and the high cost of processing. Until 1980, 5–50% of butter clam production was from the Strait of Georgia; since then, it has generally been over 80% (Fig. 2).

Harvest of littleneck and manila clams was generally low until the mid-1970s, when markets began to demand steamer clams. Since then, landings of both species, particularly manila clams, have increased, and they are now the dominant species in the fishery (Fig. 2). The Strait of Georgia has always been an important harvesting area for both species. Generally, over 60% of the littleneck and over 80% of the manila clam catch have been from the strait. The situation for mixed clams is similar to that for littleneck and manila clams.

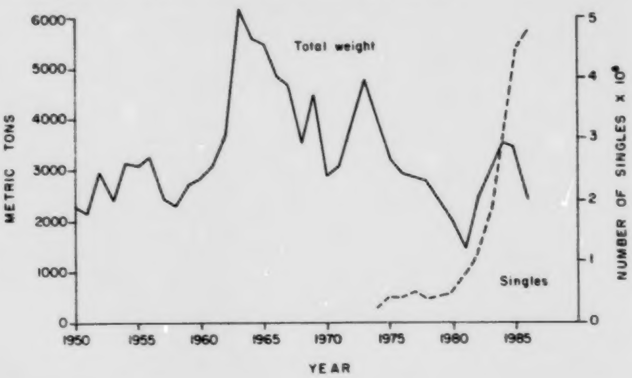
Management of intertidal clams is by size limit: 63-mm shell length for butter clams and 38-mm shell length for littleneck and manila clams.

Subtidal fisheries for geoducks and horse clams are recent (Fig. 3). Harvesting is by divers equipped with scuba or hookah (Harbo and Peacock 1983; Harbo *et al.* 1986). Initially a large part of the catch was from the Strait of Georgia, but recently this area has provided less than 20% of the total catch. Horse clams have been harvested intertidally (Quayle and Bourne 1972), but more recently the fishery has been for subtidal stock by geoduck divers. Landings have been small and almost entirely from the strait. Management of the geoduck fishery is by limited entry into the fishery and area quotas.

The Pacific oyster industry is essentially a culture industry undertaken in areas leased from the provincial government (Quayle 1969*b*, 1988). Most production is from intertidal bottom culture, but recently some production has been from hanging or floating culture, particularly for single oysters for the half-shell trade (Quayle 1971). Landings have ranged from 1000 to 6000 t whole weight (Fig. 4), and over 90% of this production has been from the Strait of Georgia.

Attempts have been made to harvest wild populations of blue mussels, but they have been unsuccessful because of poor quality and low prices. Recently there have been attempts to culture mussels, but production has been small (Table 1).

Figure 4
Landings of Pacific oysters in British Columbia, 1951–86



The fishery for pink and spiny scallops is small (Table 1). Some harvest is by small boats with homemade trawls, but most of the catch is by divers. Almost the entire catch is from the Strait of Georgia. Management is by a size limit, a 60-mm shell height minimum.

Bivalves, particularly intertidal clams, are also harvested in the recreational fishery (Carmichael and Bourne 1986; Bourne *et al.* 1987). Species harvested are generally the same as in the commercial fishery. The extent of landings in the recreational fishery is unknown, but landings are probably extensive, particularly in the Strait of Georgia where numbers of residents and tourists are high (Bourne *et al.* 1987).

Bivalves are eaten by many species of birds, including ducks, gulls, oystercatchers, and even crows (Cottam 1939; Hartwick 1976; Vermeer and Levings 1977; Vermeer 1981, 1982*a*, 1982*b*, 1983; Vermeer and Bourne 1984; Bourne 1984; Richardson and Verbeek 1987; Vermeer and Ydenberg, this publication). Small bivalves may be of some importance in the diet of various species of waders.

Glaucous-winged Gulls feed on cockles, manila clams, and mussels (Vermeer 1982*b*; unpubl. data). Both species of clams are buried at shallow depths in the substrate and are easy prey for gulls. Gulls are frequently observed flying with bivalves in their bills and dropping them on specific rocks to break the shells, then landing to eat the soft parts. Glaucous-winged Gulls often follow clam diggers during daylight tides and will feed on clams left behind by diggers. However, in the Strait of Georgia much of the food of Glaucous-winged Gulls is obtained by scavenging human refuse (Vermeer 1982*b*). Glaucous-winged Gulls are probably not serious predators of commercially important bivalves in the strait, but they may be a significant predator on cockles. Commercially important bivalves are probably of minor importance to other species of gulls, and predation by oystercatchers is probably minor.

In the Strait of Georgia, most bird predation on bivalves is by several species of ducks, including Bufflehead, Barrow's Goldeneye, Common Goldeneye (*B. clangula*), Greater Scaup (*Aythya marila*), Oldsquaw (*Clangula hyemalis*), Harlequin, and three species of scoters—White-winged, Surf (*Melanitta fusca*), and Black (*M. nigra*). Wintering flocks of these ducks feed extensively on organisms in the intertidal areas of the strait. During fall and winter, low tides in the strait occur only at night, and intertidal areas are covered with water during daylight hours but are well within the diving range of these ducks.

Most wintering ducks in the Strait of Georgia appear to be omnivorous in feeding habits and eat a wide variety of bivalves, but some species appear to target on specific bivalve species. The most commonly eaten bivalve species is the blue mussel. Buffleheads, Common and Barrow's goldeneyes, Greater Scaup, Oldsquaws, and Harlequin Ducks do not appear to feed extensively on buried clams in the strait. Commercially valuable species eaten are mostly littleneck and manila clams. Scoters, particularly White-winged and Surf, appear to target on intertidal clams—mostly littleneck and manila clams—when feeding in the intertidal area (Bourne 1984). These clam species are probably preferred because they occur at shallow depths in the substrate. Horse clams are rarely eaten, and geoducks have not been reported in the gut contents of ducks, probably because they are deep in the substrate.

Greater Scaup have been observed feeding on oysters in the Strait of Georgia (D.B. Quayle, pers. commun.), but they are probably not a serious predator on oysters—except under special circumstances—because of methods of culture. Few single oysters are found in the strait; they are usually attached to old shell or occur in clumps of two or more, probably too large for ducks to ingest. Heavy predation by ducks would occur only in areas where there are large numbers of small single oysters.

Scallops have not been recorded in the gut contents of sea ducks in the Strait of Georgia, presumably because they occur at water depths too deep for them to be a suitable prey.

Ducks can be important predators of marine bivalves. Bourne (1984) estimated that a flock of 200 scoters could consume between 5.3 and 15.9 t of littleneck and/or manila clams in a six-month period. Campbell *et al.* (1987) estimated that a flock of 3000 ducks could consume 45 t of manila clams each year in an inlet in Puget Sound.

Ducks may cause another problem with harvesting bivalves. Feces from flocks of ducks can cause fecal contamination of bivalves, making them unfit for human consumption and requiring closure of the area to clam harvesting (Bidwell and Kelly 1950). This is the reported cause of the present closure of clam beaches in the Hammond Bay area near Nanaimo. Such contamination could be an important consideration in aquaculture operations.

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Benthos available as food for marine and shoreline birds in the Strait of Georgia

Colin D. Levings

1. Abstract

The availability of benthic invertebrates used as food by birds along the shorelines of the Strait of Georgia is strongly related to the sediment preferences and depth distributions of the communities involved. Tides, as well as seasonal and long-term fluctuations in population density of the invertebrates, can also affect the timing and amount of available benthic food.

The sand and marsh intertidal flats at the mouth of the Fraser River and Boundary Bay are recognized as particularly significant feeding areas characterized by soft sediments. Shorebirds such as plovers and sandpipers feed on invertebrates (e.g., *Corophium* spp., Amphipoda) found in abundance on tide flats. These organisms are available to the birds only at low tide or when there is a very shallow layer (<5 cm) of water over the flats. Larger predatory birds such as Great Blue Herons (*Ardea herodias*) can utilize larger invertebrate prey such as crabs (e.g., *Cancer magister*, *C. productus*) on the flats but can feed when the water is deeper. Diving ducks can forage over the flats when the tide is high and can also use shallow subtidal habitats. Bivalve molluscs such as cockles (*Clinocardium nuttallii*) and clams (e.g., *Protothaca staminea*, *Mya arenaria*) are commonly eaten.

Overwintering ducks such as scoters and goldeneyes feed on rocky shore fauna at high tide and can also dive subtidally for food. Because most of the shoreline of the Strait of Georgia is rocky, it is an important habitat for management of bird populations. Epifauna such as barnacles (*Balanus glandula*), mussels (*Mytilus edulis*), and oysters (*Crassostrea gigas*) are available in the shallow littoral areas, except near river mouths, where salinity probably limits their distribution. Larger epifauna such as starfish (*Pisaster ochraceus*) are also available and are occasionally used by Glaucous-winged Gulls (*Larus glaucescens*). Gastropod molluscs such as *Lacuna* spp. and *Margarites* sp. are also abundant subtidally. Such rocky shore species are usually not tolerant of low salinity and high sediment loads, and hence their abundance usually decreases in estuaries.

Intertidal invertebrates are part of a complex nearshore food web, usually based on detritus from vascular plants (e.g., eelgrass), micro- or macrobenthic algae (e.g., bull kelp), and phytoplankton (Levings *et al.* 1983). Most of the rocky shorelines of the Strait of Georgia are still intact, but soft sediment habitats in a number of industrialized estuaries have been disrupted. Restoration has been conducted on the Fraser River estuary and elsewhere on the Pacific coast (e.g., Wilcox 1986) and may provide a useful technique to assist in managing the habitat of coastal water birds.

2. Résumé

La disponibilité des invertébrés benthiques dont se nourrissent les oiseaux le long des littoraux du détroit de Georgia est fortement liée à des préférences de sédiments et à la répartition selon la profondeur des communautés en question. Les marées aussi bien que les variations saisonnières et à long terme de la densité de population des invertébrés peuvent également avoir un effet sur la quantité de nourriture benthique et le moment où cette nourriture est disponible.

Les battures sableuses et marécageuses de la zone intertidale située à l'embouchure du Fraser et de la baie Boundary sont reconnues comme des aires d'alimentation particulièrement importantes caractérisées par des sédiments mous. Des oiseaux de rivage comme des pluviers et des bécasseaux et maubèches se nourrissent d'invertébrés (par ex. : *Corophium* spp., Amphipoda) présents en abondance sur les battures. Les oiseaux peuvent s'en nourrir seulement à marée basse ou lorsque les battures sont recouvertes d'une couche d'eau très peu profonde (<5 cm). De gros oiseaux prédateurs comme les Grands Hérons (*Ardea herodias*) peuvent rechercher comme proies de gros invertébrés comme des crabes (*Cancer magister*, *C. productus*) sur les battures mais peuvent se nourrir lorsque la couche d'eau est plus épaisse. Des canards plongeurs peuvent rechercher leur nourriture sur les battures à marée haute et peuvent aussi utiliser des habitats infratidaux. Des bivalves comme des coques (*Clinocardium nuttallii*), des palourdes et des myes (par ex. : *Protothaca staminea*, *Mya arenaria*) servent couramment de proie.

Les canards qui hivernent comme les macreuses et les garrots se nourrissent d'organismes se trouvant sur la côte rocheuse à marée haute et peuvent aussi plonger dans la zone infratidale pour trouver leur nourriture. Parce que presque tout le littoral du détroit de Georgia est rocheux, il constitue un habitat important pour la gestion des populations d'oiseaux. Des épibiontes comme les balanes (*Balanus glandula*), les moules (*Mytilus edulis*) et les huîtres (*Crassostrea gigas*) sont disponibles dans les zones littorales peu profondes, sauf près de l'embouchure des cours d'eau où la salinité limite probablement leur répartition. Des épibiontes plus gros comme l'étoile de mer *Pisaster ochraceus* sont également disponibles et ils sont parfois la proie des Goélands à ailes grises (*Larus glaucescens*). Des gastropodes comme *Lacuna* spp. et *Margarites* sp. abondent également

dans la zone infratidale. Ces espèces qui fréquentent les côtes rocheuses ne tolèrent pas en général les eaux de faible salinité et dont la charge en sédiments est élevée, et leur abondance diminue donc en général dans les estuaires.

Les invertébrés de la zone intertidale font partie d'un réseau trophique côtier complexe, reposant en général sur les déchets de plantes vasculaires (zostères marines), d'algues micro- ou macrobenthiques (comme l'algue brune *Nereocystis*) et du phytoplancton (Levings *et al.*, 1983). Presque tous les littoraux rocheux du détroit de Georgia sont encore intacts, mais les habitats se trouvant dans les sédiments mous de plusieurs estuaires industrialisés ont été perturbés. Le rétablissement a été effectué dans l'estuaire du Fraser et dans d'autres zones sur la côte du Pacifique (par ex. : Wilcox, 1986) et il peut constituer un moyen utile pour aider à la gestion de l'habitat des oiseaux aquatiques côtiers.

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Distribution, abundance, and habitat of prey fishes in the Strait of Georgia

Douglas E. Hay, Michael C. Healey, Laura J. Richards, and Jeffrey B. Marliave

1. Abstract

The distribution, abundance, and habitat of the major fish species in the Strait of Georgia are reviewed in the context of their vulnerability to seabird predation. The fish fauna is classified into four groups:
(1) mainly schooling migratory species, including herring, smelts, and juvenile salmonids, that have dense, localized distributions and leave the Strait of Georgia for extensive periods;
(2) nearshore, shallow-water species, including rockfishes, perches, and greenlings, that are nonmigratory and have widespread but relatively low-density distributions;
(3) mainly intertidal and shallow subtidal fishes that have a widespread, low-density distribution, although the cumulative abundance is substantial; and
(4) abundant, deep-water species, including the Pacific hake (*Merluccius productus*) and walleye pollock (*Theragra chalcogramma*), that may be vulnerable to seabird predation for short periods during their larval and juvenile stages, which occupy shallow water.
The migratory fishes, especially adult herring and juvenile salmon, are among the most numerous and abundant potential prey, but their distribution and abundance vary substantially within and among years, so that their predators would be forced to be opportunistic. Juvenile herring, resident in the Strait of Georgia during their first year of life, probably are the most important prey of seabirds. Sandlance are also important, but very little is known about them. Analyses of diets of seabirds may not necessarily reflect relative species abundance; several factors, including fishing activities, can lead to increased vulnerability.

2. Résumé

La distribution, l'abondance et l'habitat des principales espèces de poisson dans le détroit de Georgia sont examinés du point de vue de leur vulnérabilité à la prédation par les oiseaux marins. Les poissons sont classés en quatre groupes. Le premier comprend surtout des espèces migratrices voyageant par bancs, y compris le hareng, l'éperlan argenté et le saumoneau, qui vivent en grand nombre dans certaines zones et quittent le détroit de Georgia pour de longues périodes. Le deuxième est formé d'espèces non migratrices, y compris les scorpènes, les ditrèmes et les lingues, qui vivent un peu partout, en nombre relativement peu élevé, près du littoral et dans les eaux peu profondes. Le troisième groupe comprend surtout des poissons qui vivent un peu partout, en petit nombre, dans la zone intertidale et la zone infralittorale peu profonde, mais dont la population totale est importante. Dans le quatrième groupe, on trouve de nombreuses espèces de poissons d'eau profonde, y compris le merlu du Pacifique (*Merluccius productus*) et le lieu de l'Alaska (*Theragra chalcogramma*); pendant de courtes périodes de leur vie larvaire et juvénile, en eau peu profonde, ces poissons peuvent être vulnérables à la prédation par les oiseaux marins. Les espèces migratrices, notamment le hareng adulte et le saumoneau, comptent parmi les proies les plus abondantes, mais comme leur distribution et leur nombre varient considérablement d'une année à l'autre et au cours de la même année, les prédateurs doivent faire preuve d'opportunisme. Le hareng juvénile, qui passe la première année de sa vie dans le détroit de Georgia, est probablement la proie la plus importante des oiseaux marins. Le lançon est également important, mais on ne sait que très peu de choses à son sujet. L'analyse du régime alimentaire des oiseaux marins n'indique pas nécessairement l'abondance relative d'une espèce; plusieurs facteurs, dont les activités halieutiques, peuvent accroître la vulnérabilité du poisson.

3. Introduction

There are more than 200 species of fishes along the BC coast, and about 180 occur, for at least short periods, in the Strait of Georgia (Hart 1973). Of these, about 100 species are sufficiently small and vulnerable to be considered as potential prey species for birds. However, most bird predation is probably confined to a relatively few species.

From the perspective of an avian predator, the Strait of Georgia fish fauna is characterized by seasonal and geographic variation in species composition, abundance or availability, and size composition. These factors are considered in this paper, which provides:
(1) an overview of the relative distribution of young or small fishes (i.e., 5–30 cm) that occur in the Strait of Georgia at locations and depths such that they would be vulnerable to seabird predation; and
(2) simple descriptions of the main habitats of the most common species.
At the end, we draw some generalized conclusions about the fish community and its characteristics relative to avian predation.

Previous summaries of fishes in the Strait of Georgia have concentrated on the commercially fished segments of the fish community (Ketchen *et al.* 1983) or on the biomass relative to primary productivity (Parsons *et al.*

1970). In this paper, we examine the seasonal distribution, abundance, and size composition first by species or groups of species. For convenience, we have arbitrarily classified the marine fish community into four major divisions:

(1) shallow-depth schooling fishes;
(2) shallow-water inshore fishes;
(3) intertidal and shallow subtidal fishes; and
(4) deep-water fishes.

The information used to assemble this paper was drawn from a variety of sources, including previously unpublished data, existing literature, personal observations, and observations by colleagues. This treatment cannot provide a complete summary of all available information about each species. For more detailed reviews of particular species or habitat types, readers should consult the cited literature or specialized works such as those by Hart (1973) or Garrison and Miller (1982). Also, it should be emphasized that some of the information we present and conclusions we draw could change with further information. If this paper serves no other purpose than to illustrate the paucity of vital information on many of our local fish species, then perhaps the preparation will have been worthwhile.

4. Shallow-depth schooling fishes

There are 10 to 12 species of small schooling fishes that are present and sometimes abundant in the shallow waters (i.e., less than 50 m from the surface) of the Strait of Georgia. Within this group we include the clupeids (herring, anchovies), the osmerids (smelts), the salmonids (including trouts, salmon, and char), the sandlance, and the sticklebacks.

4.1. Pacific herring (*Clupea harengus*)

It is not generally appreciated that the Pacific herring found in the Strait of Georgia is basically a migratory species. It spawns in intertidal and shallow subtidal areas, particularly on the Vancouver Island side (Fig. 1) in March; it then returns to waters off the west coast of Vancouver Island, where it spends the summers (Taylor 1964; Hay *et al.* 1987). In the late fall and early winter, herring returns to the Strait of Georgia, through the Strait of Juan de Fuca and Johnstone Strait (Fig. 1). At that time, it tends to gather in dense concentrations that are generally inaccessible to seabirds.

The migratory behaviour of Pacific herring in the Strait of Georgia occurs among sexually maturing fish in their third year (age 2+) of life, but the migratory habits of younger herring are less certain. The younger stages (ages 0+ and 1+) do not appear to move in and out of the strait as readily as the older fish (Hay 1985). This is an important point relative to seabird predation, because it seems that the prerecruit herring are not migratory and thus are available as seabird prey throughout the year. The distribution of juvenile herring within the Strait of Georgia (Fig. 2) appears to be mainly in nearshore waters (Hourston 1951, 1958).

Herring are the most abundant migratory fish in the Strait of Georgia. The biomass of spawning herring in the strait can be estimated with reasonable accuracy (Haist *et al.* 1987; Hay and Kronlund 1987). Stock assessment methods rely on three distinct types of data:

(1) annual catch;
(2) annual age composition and related information on length and weight at age; and
(3) estimates of the annual spawn deposition.

Spawning occurs inter- and subtidally. Using the age structure analysis, and assuming a constant survival (about 0.65) during the juvenile and prerecruit stages, Haist *et al.* (1987) estimated numbers of herring during their first (age 1) and second (age 2) years of life. Numbers of age 0+ fish ranged from about 0.2 to 3.3 billion, and age 1+ fish from about 0.15 to 2.1 billion over the period from 1951 to 1986 (Appendix Tables 2.6 and 2.7, Haist *et al.* 1987). Also, herring stock biomass fluctuates substantially over time.

Herring are probably the single most important prey species for seabirds. However, most predation would be confined to the juvenile stages, at age 0+ or 1+. Most older age-classes migrate out of the Strait of Georgia following spawning in March and do not return until early winter (Taylor 1964; Hay 1985), although the precise size or age when herring begin offshore migrations is unknown. When migratory herring return to the strait, they tend to confine themselves to a relatively few deep areas, generally inaccessible to seabirds, until they move into shallow water prior to spawning.

There may be certain locations within the Strait of Georgia where there are local or nonmigratory herring stocks that provide adult prey throughout the year. The status of such stocks is uncertain, but it is possible that resident stocks might be present in the southern Gulf Islands, the Sechelt area, Baynes Sound, and southern Johnstone Strait (Fig. 1) (Hay 1986).

4.2. Pacific sandlance (*Ammodytes hexapterus*)

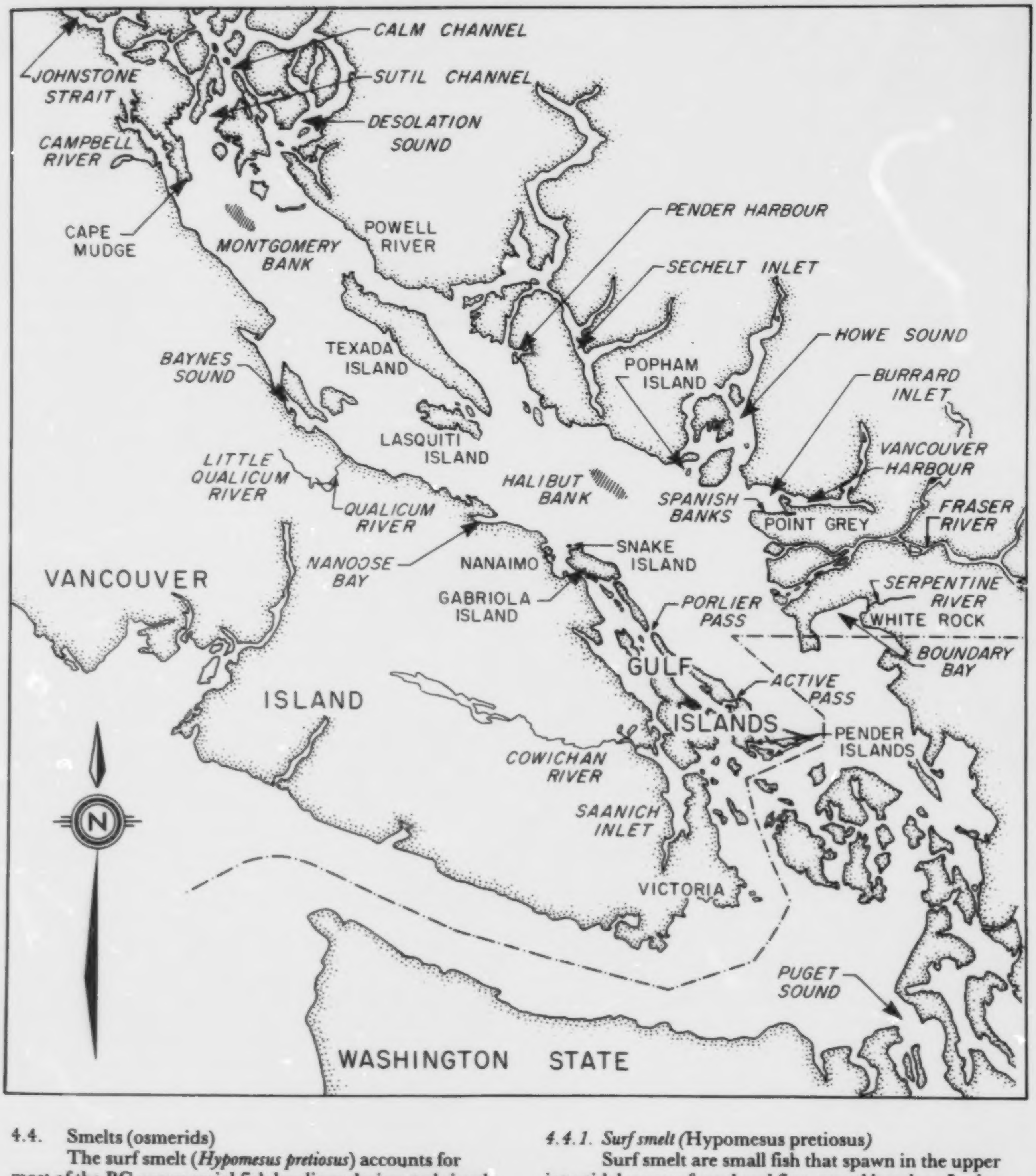
The Pacific sandlance does not fit easily into any category. It is often a shallow-water species, but frequently it inhabits deeper water. We know very little about this species in local waters. Based on examination of gut contents of avian and fish predators, sandlance frequently are present and are a major component of diets (Westrheim and Harling 1983; Vermeer and Westrheim 1984). Sandlance spawns during late winter and early spring, and its larvae are common in nearshore waters in March, April, and May, at which time they provide a substantial source of food to seabirds.

4.3. Northern anchovy (*Engraulis mordax*)

Northern anchovy are distributed from Baja California, Mexico, to the Queen Charlotte Islands (Hart 1973). They are a small, pelagic schooling species. Most live 3–4 yr, reaching an average length of about 15 cm, mature in their second year, and spawn in July and August (Pike 1951). Little is known about their biology in local waters, but the species is under intense investigation in California, where it supports large fisheries. In British Columbia, anchovy occur on banks off the west coast of Vancouver Island and often in shallow water very close to shore. Larval anchovy sometimes occur in the Strait of Georgia, but adult abundance appears to be low and irregular. At the present time, accurate stock assessments are not available.

Anchovy catches appear to fluctuate over time. Anchovy are subject to sudden changes in abundance, probably caused by environmental factors. Some fishermen regard anchovy as a nuisance, because they sometimes become gilled in seine webbing and cause serious fouling problems. With few exceptions, anchovy in British Columbia are not sold commercially. Most unintentional encounters with commercial fishing gear could leave some anchovy dead or injured and accessible to avian predators.

Figure 1
The Strait of Georgia showing approximate locations of geographic names mentioned in the text


CALM CHANNEL
JOHNSTONE STRAIT
SUTIL CHANNEL
DESOLATION SOUND
CAMPBELL RIVER
CAPE MUDGE
MONTGOMERY BANK
POWELL RIVER
PENDER HARBOUR
SECHELT INLET
HOWE SOUND
TEXADA ISLAND
BAYNES SOUND
POPHAM ISLAND
BURRARD INLET
LASQUITI ISLAND
LITTLE QUALICUM RIVER
HALIBUT BANK
VANCOUVER HARBOUR
SPANISH BANKS
QUALICUM RIVER
POINT GREY
FRASER RIVER
NANOOSE BAY
NANAIMO
SNAKE ISLAND
VANCOUVER
GABRIOLA ISLAND
PORLIER PASS
SERPENTINE RIVER
WHITE ROCK
BOUNDARY BAY
GULF
ACTIVE PASS
ISLAND
ISLANDS
PENDER ISLANDS
COWICHAN RIVER
N
SAANICH INLET
VICTORIA
PUGET SOUND
WASHINGTON STATE

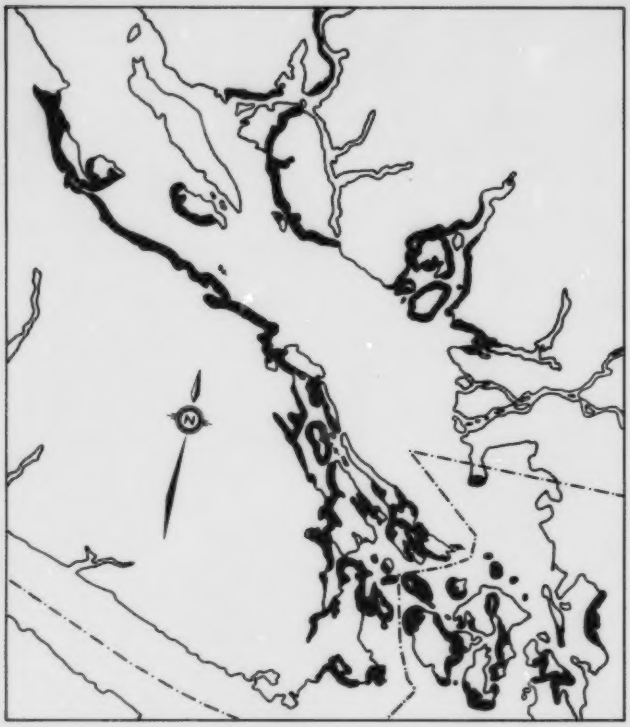
4.4. Smelts (osmerids)

The surf smelt (*Hypomesus pretiosus*) accounts for most of the BC commercial fish landings designated simply as "smelt." However, several other species of smelt (Osmeridae) occur in the Strait of Georgia, including the eulachon (*Thaleichthys pacificus*), the capelin (*Mallotus villosus*), and the longfin smelt (*Spirinchus thaleichthys*). The last two species occur in insignificant quantities.

*4.4.1. Surf smelt (*Hypomesus pretiosus*)*

Surf smelt are small fish that spawn in the upper intertidal zones of sand and fine-gravel beaches. In the Strait of Georgia, they spawn during the summer months along the sandy beaches of Point Grey and White Rock (Fig. 2) (Hart and McHugh 1944). Most spawning occurs at mid- and late summer. The fish are vulnerable to capture at this time, and in some locations small local fisheries

Figure 2
Nearshore distribution of juvenile herring in the Strait of Georgia (from Hourston 1956)



have developed. Some individuals may mature in their first year; most are mature at age 2. The fish do not appear to survive much longer than 3 yr or grow much beyond 20 cm in total length. In the strait, surf smelt are known to occur mainly near Vancouver, where they spawn on local beaches (Spanish Banks, Kitsilano). The abundance of surf smelt in BC waters is largely unknown, but probably does not exceed a few thousand tonnes.

4.4.2. *Eulachon (*Thaleichthys pacificus*)*

The eulachon is a small anadromous species of smelt. It spawns in the lower reaches of large rivers on the BC coast, particularly the Fraser River. Spawning occurs in the spring months, mainly mid-March to mid-May (Samis 1977). After spawning, eulachon eggs incubate in coarse sand and gravel in the lower Fraser River bottom for up to one month. Larvae are flushed into the sea within a few days. Larval and juvenile eulachon are common in nearshore waters throughout the province and have been reported in catches on offshore banks. After 2–3 yr, most fish reach an average size of about 20 cm when sexually mature. There frequently is a substantial mortality after spawning, but some individuals are repeat spawners.

Catch trends during the 1970s and 1980s are lower than those during the mid-1960s, when the average annual reported catch was about 100 t (Samis 1977). However, much larger catches occurred in the 1950s, over 340 t being taken in 1952 (Ricker *et al.* 1954). These fluctuations over time could reflect different factors, such as changes in abundance, inconsistent fishing effort, or inconsistent catch records. Natural environmental factors may also affect abundance, and there appears to be an inverse relationship between the magnitude of the freshet of the Fraser River and the year-class strength (Ricker *et al.* 1954).

4.5. Threespine stickleback (*Gasterosteus aculeatus*)

The threespine stickleback is ubiquitous throughout north Pacific nearshore marine habitats and freshwater drainages (Hagen 1967; Miller and Hubbs 1969), including the Strait of Georgia. Unfortunately, there are no estimates of its biomass in marine habitats. In freshwater systems it sometimes can be very abundant, and marine forms of this species appear to be equally common in some shallow, tidal habitats. There are large anadromous populations of sticklebacks that spawn in the lower reaches of the Fraser River. These fish may be especially vulnerable to seabird predation during their spawning migrations and during the breeding season when males defend territories and build nests in shallow water.

4.6. Salmonids

Three genera and 10 species of the family Salmonidae are found in the Strait of Georgia and connecting marine waterways (Hart 1973). All these species are anadromous. They migrate to sea as juveniles and return to fresh water to spawn when mature. All five species of Pacific salmon (*Oncorhynchus* spp.) die after spawning, but the trouts (*Salmo*) and char (*Salvelinus*) may spawn repeatedly.

Only the distribution and abundance of juvenile salmon during their first year in the ocean will be considered here. Later in life, the fish are too large for most marine birds to capture and subdue. Emphasis will be on the juveniles of Pacific salmon, as the other species are comparatively rare in marine waters. The juveniles of all species occupy the surface waters, especially the first few metres. During at least part of their early sea lives, they are found very close to shore. Mortality of all species during their first summer of ocean life is believed to be high. The agents of this mortality are not well known, but predatory fishes and marine birds are important (Simenstad *et al.* 1979; Robinson *et al.* 1982; Mace 1983; Vermeer *et al.* 1987).

4.6.1. *Sockeye salmon (*O. nerka*)*

Most sockeye salmon in the Strait of Georgia come from the Fraser River, which produces 40 to 200 million smolts each year (estimated from escapements to the Fraser River ranging from 0.8 to 4.0 million and an assumption of 100 smolts produced per female). A few sockeye salmon are also produced in other BC mainland rivers, and some probably migrate north into the strait from Puget Sound. Sockeye salmon enter the strait from the spawning rivers, mainly in April and May, as smolts aged 1+ or 2+ and 80–100 mm long. A few sockeye salmon from the Fraser River rear as fry from March through June in the Fraser River delta and enter the strait in July when about 70 mm long (Healey 1980*a*).

Sockeye salmon entering the Strait of Georgia from the Fraser River are swept north or south of the river mouth, or across the strait and into the Gulf Islands, by the river plume. On the mainland shore, the smolts apparently begin immediately moving north and northwest across the entrance to Burrard Inlet and Howe Sound and up the mainland coast. Smolts swept into the Gulf Islands area congregate principally around North and South Pender Islands and west of Gabriola Island; then they begin moving north diagonally across the strait to join those migrating along the mainland coast in the vicinity of Texada and Lasquiti islands (Fig. 1). By late May, the smolts are distributed in a band from the Gulf Islands to Texada Island and along the mainland coast from Howe Sound north to

Calm and Sutil channels (Fig. 1). By mid-June, the number of sockeye salmon in the strait has begun to dwindle, and by early July almost all have left the strait. However, small numbers, mostly underyearling smolts, can be found in the strait throughout the summer (Healey 1978, 1980*a*; Groot and Cooke 1987).

*4.6.2. Pink salmon (*O. gorbuscha*)*

Juvenile pink salmon are abundant in the Strait of Georgia only in even-numbered years, when 100 to 400 million (average 225 million) are produced from the Fraser River (Bailey 1979). During odd-numbered years, no pink salmon fry are produced from the Fraser River, and probably not more than 10 million from other tributaries. Pink salmon migrate to sea as fry about 35 mm long, mainly from March through May. During their first few weeks of ocean life, pink salmon fry congregate in sheltered marine bays close to shore but seem to avoid brackish water habitats close to river mouths. As they grow, they move away from shore into deeper water and by June are most abundant in the pelagic zone. Because of the importance of the Fraser River as a source, pink salmon are most abundant in the southern half of the Strait of Georgia from April until June. Most leave the strait in late June or early July, perhaps because feeding conditions have become poor (Healey 1982*a*). Occasionally, however, substantial numbers of pink salmon are observed within the strait and adjacent waterways in late August or September.

Survival of pink salmon fry during their early sea lives is poor. Parker (1968) estimated that only 23–45% of pink salmon fry from the Bella Coola River system survived their first 40 d at sea. Assuming similar survival rates for the Strait of Georgia, perhaps fewer than 30% of the fry that enter the strait in April and May survive to leave in June or July.

*4.6.3. Chum salmon (*O. keta*)*

Chum salmon are produced from all major and most of the minor rivers flowing into the Strait of Georgia. Total production is about 240 million, of which about 100 million come from the Fraser River. This estimate is based on fry enumeration in the Fraser River (Bailey 1979) and potential egg deposition and survival in other systems (i.e., fry = 0.5 [proportion females] × 3000 [eggs/female] × 0.15 [egg to fry survival]). Chum salmon are also produced from BC hatcheries, and about 80 million are released into tributaries of the strait annually (SEP 1984).

Like pink salmon, chum salmon migrate to sea as fry (40 mm long), mainly from March to May. Early in their ocean lives, chum salmon occupy sheltered marine bays, where they intermingle with pink salmon fry. Unlike pink salmon, however, chum salmon also occupy brackish water habitats near river mouths as well as freshwater delta habitats in the Fraser River (Healey 1979; Levy and Northcote 1982). As they grow, chum salmon move away from shore into the pelagic zone, where they are abundant for about two months. Chum salmon migrate from the Strait of Georgia mainly in late June or July, possibly because feeding conditions become poor (Healey 1982*a*). After July, chum salmon juveniles are generally rare in the strait, although occasionally large schools have been observed in the late summer and autumn in adjacent waterways (e.g., Hartt and Dell 1986).

Chum salmon probably suffer mortality rates comparable to those of pink salmon of similar size. Consequently, only about 30% of the fry that enter the Strait of Georgia between March and May survive to leave in June or July.

*4.6.4. Coho salmon (*O. kisutch*)*

Coho salmon, like chum salmon, are produced from all the major and most of the minor rivers flowing into the Strait of Georgia. Total production is much less than that of any of the three salmon species mentioned so far. The size of this production cannot be estimated with any degree of confidence, however, because estimates of spawning escapement for this species are very uncertain. Reported spawning escapement averaged 191 000 over the 5-yr period 1978–82; this escapement would yield total wild production in the order of 7 million (assuming a 1:1 sex ratio and a smolt production of about 75 per female). The reported spawning escapement is almost certainly an underestimate, however, perhaps by as much as an order of magnitude. Wild smolt production could, therefore, be much greater than 7 million. Coho salmon are also produced from British Columbia's hatcheries, and annual release of smolts into the Strait of Georgia are in the order of 10 million (SEP 1984). Also, many coho salmon juveniles from Puget Sound move into the southern strait during the summer (Mathews and Buckley 1976).

Coho salmon migrate to sea mainly in May and June after 1 or 2 yr in fresh water and apparently disperse rather widely in the Strait of Georgia. Although an uncertain and variable proportion of juveniles leaves the strait sometime in the summer or autumn, many coho salmon remain in the strait throughout their marine lives. Catches in the Gulf Islands indicate a relatively constant abundance throughout the summer and autumn, at least in this region of the strait (Table 1).

Sampling throughout the Strait of Georgia in late summer of 1975 and 1976 showed that coho salmon were most abundant in the Gulf Islands region and also relatively more abundant along the Vancouver Island shore than along the mainland. The species was, however, common everywhere. In the winter of 1974, samples taken around the Gulf Islands and north along the Vancouver Island shore to Baynes Sound showed that coho salmon were most abundant in Saanich Inlet (Fig. 1) (Healey 1978). As previously mentioned, mortality of coho salmon during their first summer at sea may be as high as 2% per day (Mathews and Buckley 1976). During their first six months in the ocean, 90% of coho salmon may be lost to predation or disease. Changes in catch rates in the Gulf Islands region throughout the summer months do not, however, reveal a significant decline in abundance. If rates of mortality are as high as Mathews and Buckley (1976) suggest, there must have been continuous immigration to this area.

Coho salmon are about 100–110 mm long when they migrate to sea. During their first summer in the Strait of Georgia, they appear to grow about 1 $mm \cdot d^{-1}$ (Mathews and Buckley 1976; Healey 1980*a*), so that by autumn they are over 200 mm long. There also appears to be some size segregation within the strait, larger juveniles being found in the north.

*4.6.5. Chinook salmon (*O. tshawytscha*)*

Chinook salmon are produced from most of the medium to large river tributaries in the Strait of Georgia, but the Fraser River is by far the largest producer. Chinook salmon are the least abundant of the five species of

Table 1
Catch-per-set and average length (cm) of juvenile salmon captured in the Gulf Islands region, May–October 1976

Species/Parameter	Month					
	May	June	July	Aug.	Sept.	Oct.
Chum						
Mean catch	4.5	138	71.0	2.8	1.3	1.8
Range of catch	0–40	0–2700	0–240	0–20	0–39	0–80
Mean length	7.2	8.8	10.1	11.2	15.4	18.2
Pink						
Mean catch	1.6	660	7.4	10.9	23.5	0.3
Range of catch	0–33	0–9900	0–25	0–89	0–509	0–8
Mean length	3.6	7.9	8.5	11.1	14.7	19.3
Coho						
Mean catch	6.0	1.3	5.9	5.2	6.0	1.2
Range of catch	0–109	0–6	0–75	0–25	0–200	0–15
Mean length	11.6	16.8	18.7	21.2	26.3	28.1
Chinook						
Mean catch	0.0	1.7	2.1	2.0	2.8	1.7
Range of catch	–	0–26	0–11	0–14	0–20	0–13
Mean length	–	13.2	15.9	13.9	21	21.5
Sockeye						
Mean catch	6.3	7.3	1.4	0.0	0.02	0.10
Range of catch	0–102	0–53	0–15	–	0–1	0–3
Mean length	10.6	10.8	11.7	–	16.0	18.5

Pacific salmon as adults and are probably also the least abundant as juveniles. Chinook salmon display a complex variety of juvenile life-history patterns, and the proportion of juveniles adopting a particular pattern is unknown for most populations. Thus, estimating total juvenile production is virtually impossible with present information. We do know that chinook salmon can at times be a dominant component of the salmonid fish fauna, particularly in estuarine habitats (Healey 1980*b*, 1982*b*). Chinook salmon are also produced in BC hatcheries, and hatchery releases into tributaries of the Strait of Georgia are in the order of 13 million (SEP 1984).

There appear to be three basic patterns of juvenile behaviour among chinook salmon (Healey 1980*a*, 1980*b*, 1982*b*). Some chinook salmon migrate to the river estuary from March to May, immediately after emerging from the gravel spawning nests, and reside in the estuary for three to six weeks before dispersing seaward. Others reside in their natal river for about two months and migrate to sea in June. A few chinook salmon, principally in the largest rivers, remain a full year in fresh water before migrating to sea in April or May.

Yearling smolts leave the Strait of Georgia rather quickly, bound for the open north Pacific Ocean, but these represent a small component of the juvenile population to begin with (Healey 1980*b*, 1983). The two types of under-yearling smolts remain within the strait in significant numbers throughout their first summer and autumn (Table 1), with possibly an out-migration from the strait in November (Healey 1980*b*).

Chinook salmon fry migrating to estuarine nursery areas are about 40 mm long. They were abundant in all the estuaries sampled in the Strait of Georgia that possess well-developed intertidal marshes (Healey 1982*b*). Chinook salmon fry were also abundant in the freshwater delta of the Fraser River (Levy and Northcote 1982). They remain in the estuary until they become about 70 mm long, after which they disperse into the pelagic waters of the Strait of Georgia. Chinook salmon fingerlings that migrate to sea in June are also about 70 mm long. Fingerlings may remain in the river estuary for a few days but then disperse into pelagic waters.

4.6.6. Trouts and chars

Four species of anadromous trout (cutthroat trout [*Salmo clarki*], steelhead trout [*S. gairdneri*], Atlantic salmon [*S. salar*], brown trout [*S. trutta*]) and one char (dolly varden [*Salvelinus malma*]) are found in the Strait of Georgia. Atlantic salmon and brown trout are introduced species, whereas the others are endemic (Hart 1973). The introduction of Atlantic salmon to British Columbia in 1905 was apparently unsuccessful, as there have been no recent records of this species in the wild (Hart 1973). During the past few years, Atlantic salmon have again been brought to the Pacific coast for the salmon pen-rearing industry, so the opportunity exists for incidental occurrence of the species in the Strait of Georgia through accidental release. Brown trout were successfully established in the Cowichan and Little Qualicum rivers early in this century. Occasional anadromy by this species is suggested, as there has been some limited movement away from these rivers (Hart 1973). Neither introduced species can, however, be considered an important component of marine salmonid populations.

Cutthroat trout and dolly varden char are also rare in the marine waters of the Strait of Georgia. Anadromous cutthroat trout normally migrate to sea during their first to third years of life. They seldom migrate far from the estuary of their natal stream and often move back into the stream to feed (Scott and Crossman 1973).

Steelhead trout are the most abundant of the anadromous trout inhabiting the Strait of Georgia but are, nevertheless, rare in comparison with Pacific salmon. Steelhead trout smolts migrate to sea when aged 1–4 yr and remain 1 or more years at sea before returning to spawn. Their ocean migrations can be very extensive, and smolts may not spend much time in the strait. A few have been captured during surveys for juvenile salmon in the Fraser River plume area and among the Gulf Islands (Hart 1973; Healey 1978).

5. Shallow-water fishes: rockfishes, perches, and greenlings

Rockfishes, perches, and greenlings are permanent residents in the Strait of Georgia, although their abundance, especially in shallow waters, may vary seasonally.

5.1. Rockfishes (*Sebastes*)

Quillback rockfish (*S. maliger*) and copper rockfish (*S. caurinus*) are the most abundant species of rockfishes in the Strait of Georgia, accounting for about 86 and 14%, respectively, of the commercial catch. There are incidental catches (< 1%) of several other species, including yellowtail rockfish (*S. flavidus*), tiger rockfish (*S. nigrocinctus*), and yelloweye rockfish (*S. ruberrimus*). Quillback, copper, and yelloweye rockfish account for 54, 23, and 15%, respectively, of the rockfish catch by the sport fishery (T. Shardlow and T. Hoyt, Department of Fisheries and Oceans, Nanaimo, BC, unpubl. data), which may be a rough indicator of their relative abundance. Several other rockfish species occur in low abundance.

Rockfish are viviparous, releasing fully developed larvae. For both copper and quillback rockfish, parturition occurs between about March and May (Echeverria 1987). Postlarval young-of-the-year (YOY) copper rockfish settle from the plankton in late July and early August. A scuba survey, conducted between August and October 1985 at Snake Island near Nanaimo, was designed specifically to measure habitat use and density of YOY copper rockfish (Haldorson and Richards 1987). In late August, density in the *Nereocystis* habitat reached 146 fish per 100 m^2 (Table 2), with most of the fish in the kelp canopy near the water surface. At that time, they would be especially vulnerable to bird predation. As the kelp began to decay, the YOY rockfish moved into demersal habitats with perennial macrophytes (*Agarum* and eelgrass).

Rockfish are long-lived species with ages of up to 55 yr for quillback rockfish and 35 yr for copper rockfish (Richards and Cass 1987). Copper rockfish appear to have a faster growth rate and mature at an earlier age. Quillback rockfish are most abundant over depths of 21–60 m (Richards 1986), whereas copper rockfish are rare below 20 m (Richards and Cass 1985). At depths above 20 m, where distributions of quillback and copper rockfish overlap, copper rockfish appear to be more generally distributed. Both species are more abundant in high relief areas (Richards 1987*b*).

5.2. Perches (embiotocids)

There are four main species of perch or embiotocids: the pile perch (*Rhacochilus vacca*), kelp perch (*Brachyistius frenatus*), shiner perch (*Cymatogaster aggregata*), and striped seaperch (*Embiotoca lateralis*). Perch are viviparous (e.g., Baltz 1984). The young are morphologically similar to the adults and live in the same habitats, although the young tend to be more closely associated with the kelp understory (Ebeling and Laur 1985). There have been no specific studies on perch in the Strait of Georgia. During the scuba surveys, perch were usually observed in highly mobile, mixed-species schools near the water surface. Hence, they may be locally important for bird predation.

5.3. Greenlings (hexagrammids)

There are three main species of greenling: painted greenling (*Oxylebius pictus*), kelp greenling (*Hexagrammos decagrammus*), and lingcod (*Ophiodon elongatus*). Spawning times vary among the species, from spring–summer for the painted greenling, to October–November for the kelp greenling, and to January–February for the lingcod. Lingcod egg masses are guarded by male lingcod until the time of hatching, between March and June (Low and Beamish 1978). Postlarval lingcod are present in surface waters between April and June. Maximum densities, found in mid-May, are 0.1–1.0 fish per 100 m^2 (Cass and Scarsbrook 1984). Over the April–June period, lingcod larvae grow from about 20 to 90 mm in length and may be important bird prey at that time.

5.4. Abundance of nearshore shallow fishes

In general, adults of the rockfishes, perches, and greenlings (with the possible exception of the kelp perch and shiner perch) are too large to be important as bird prey. Rockfish and lingcod juveniles may, however, be vulnerable to bird predation. Species from all three groups are exploited by commercial and recreational fisheries in the Strait of Georgia, and the rockfish catch, in particular, has been increasing in the strait since about 1977 (Richards 1988). Therefore, there may be increased opportunities for seabirds to scavenge fish lost or wasted by these fisheries. In 1986, the commercial rockfish catch was about 340 t, and the sport catch was approximately 130 t (168 000 fish). Increasing catches probably reflect expanding markets, not rockfish abundance. In contrast, lingcod abundance and catches have declined recently (Richards and Hand 1988).

Composite abundance of shallow nearshore fishes at depth can be estimated roughly from scuba surveys conducted from September to November of 1984 and 1985 between Pender Harbour and Desolation Sound (Fig. 1 in Richards 1987*a*). Divers counted visible fish species, such as rockfishes and perches, observed during surveys of 50-m horizontal transects. Cryptic species such as gobies, flatfish, and sculpins were ignored because of the difficulty of obtaining reliable counts. Detailed methods for estimating rockfish, lingcod, and kelp greenling densities (except YOY rockfish) are presented in Richards (1987*a*, 1987*b*).

Abundance of rockfishes, perches, and greenlings in the Strait of Georgia (Table 3) was based on the area of rocky and gravel shoreline (Levings *et al.* 1983). The highest estimates were obtained for YOY rockfish (40–100 million) and shiner perch (20 million). However, these estimates are probably also the least accurate. Shiner

Table 2
Mean density (fish/100 m^2) and mean length (mm) of young-of-the-year copper rockfish from *Agarum*, *Nereocystis*, and eelgrass habitats near Snake Island, August–October 1985 (from Haldorson and Richards 1987)

	Fish density			Fish size		
Habitat	**Aug.**	**Sept.**	**Oct.**	**Aug.**	**Sept.**	**Oct.**
Agarum	59.4	46.4	50.8	36.5	44.6	45.6
Nereocystis	145.8	14.0	1.6	38.2	-	-
Eelgrass	74.8	135.8	67.0	38.8	46.4	48.4

Table 3
Mean density (fish/100 m²), coefficient of variation in density as a percentage of the mean, and estimated total abundance (millions of fish) in the Strait of Georgia for fish species surveyed by scuba in statistical areas 15 and 16 in 1984 and 1985[a]

	1984			1985		
Species	**Mean density (fish/100 m²)**	**CV**	**Abundance (millions)**	**Mean density (fish/100 m²)**	**CV**	**Abundance (millions)**
Embiotocidae						
Pile perch	1.94	204	7.99	1.99	191	8.23
Kelp perch	0.49	1242	2.03	0.22	2 969	0.89
Shiner perch	5.95	235	24.58	5.74	145	23.69
Striped seaperch	1.77	244	7.31	2.67	154	11.03
Hexagrammidae						
Painted greenling	0.08	6231	0.32	0.05	12 792	0.20
Kelp greenling	0.48	371	2.00	0.35	616	1.46
Lingcod	0.30	1044	1.24	0.10	3 567	0.43
Scorpaenidae						
Tiger rockfish	0.11	5628	0.44	0.01	125 424	0.04
YOY rockfish	23.28	16	96.14	10.70	34	44.17
Copper rockfish						
—small	0.67	649	2.75	0.12	4 669	0.48
—large	0.97	394	4.03	0.83	661	3.43
—combined	1.64	215	6.77	0.95	521	3.92
Quillback rockfish						
—small	2.06	139	8.53	1.44	264	5.93
—large	0.91	398	3.74	1.09	446	4.52
—combined	2.97	95	12.27	2.53	124	10.45
Combined rockfish	4.73	45	19.53	3.49	80	14.42

[a] Abundance is based on area of rocky and gravel shoreline from Levings *et al.* (1983). For copper and quillback rockfish, densities are given for three sizes: young-of-the-year (YOY), 7- to 19-cm fish, and 20+-cm fish. Combined rockfish excludes young-of-the-year.

perch and YOY rockfish were usually observed in large schools, and the surveys were designed to estimate densities of large and solitary rockfish.

6. Intertidal and shallow subtidal fishes: cottids, gobies, pholids, stichaeids, and flatfishes

6.1. Habitat

Intertidal fish assemblages in the Strait of Georgia tend to be of low diversity, with roughly five different types of habitat:

(1) Mudflats and protected soft-bottom shores with eelgrass (*Zostera marina*) beds typically have assemblages of juvenile staghorn sculpins (*Leptocottus armatus*), arrow gobies (*Clevelandia ios*), and juvenile flatfishes, including Pacific sanddab (*Citharichthys sordidus*), English sole (*Parophrys vetulus*), and starry flounders (*Platichthys stellatus*). Along with those species, the tidal flats also have gunnels living in the eelgrass itself, including the crescent gunnel (*Pholis laeta*), saddleback gunnel (*P. ornata*), and penpoint gunnel (*Apodichthys flavidus*).

(2) Protected fjord walls and rock shores of tidal passes typically have moderately dense populations of tidepool sculpins (*Oligocottus macullosus*), sharpnose sculpins (*Clinocottus acuticeps*), and flathead sculpins (*Artedius lateralis*).

(3) On cobble and boulder shores with protection from swells, northern clingfish (*Gobiesox maeandricus*) and cockscomb pricklebacks (*Anoplarchus purpurescens*) occur together with tidepool and flathead sculpins.

(4) In areas with greater exposure to swells (open fetch to the Strait of Georgia), the black prickleback (*Xiphister atropurpureus*) and rock prickleback (*X. mucosus*) are added to that same assemblage that occurs in cobble on protected shores.

(5) Exposed shores of solid rock (walls or slopes) tend to have few intertidal fish, with tidepool sculpins and flathead sculpins predominating. In the immediate subtidal region, a few more small fish species occur in certain areas and will be discussed below.

All these fishes are relatively small, at least in the life stages that occur along the shoreline (cf. those of staghorn sculpin and starry flounder juveniles). One relatively large fish that occurs intertidally is the spawning male midshipman (*Porichthys notatus*). This species nests during early summer in hollows under large rocks over soft or rocky substrate. The male tends the eggs and the attached hatchlings, which remain fixed to the rock undersurface, until they are free-swimming (Arora 1948). Because the males exhibit guarding behaviour that includes audible croaking if disturbed, it seems reasonable that birds such as Great Blue Herons (*Ardea herodias*) could learn to probe into spaces along boulder edges and discover nest-guarding males. Other life stages of this species live in deeper water.

Near seaweeds and rocks, along rocky shores of moderate exposure, schools of tubesnouts (*Aulorhynchus flavidus*) are abundant in shallow water. Because this species feeds on plankton by pipette-type suction, its schools hover in relatively stationary positions, and the schools show home-site fidelity (Limbaugh 1962). Larval and juvenile stages show the behaviour and habitat preferences of adults (Marliave 1976). Another benthic fish of extremely shallow subtidal waters along rocky shorelines is the blackeye goby (*Coryphopterus nicholsi*). This goby is territorial and spaces itself uniformly within rocky areas. Therefore, it is of rather uniform abundance in most areas having adequate subtidal cobble for excavation of spaces under the rock's edges by these gobies. The blackeye goby typically remains stationary in the vicinity of its den and is visible on the open bottom when not in hiding.

The northern clingfish is abundant on cobble shores, but the species is cryptic and the fish cling with their pelvic discs to the undersides of boulders lying on coarse grades of substrate. The larvae settle onto smooth seaweeds, however, and remain in such visually exposed positions until about 2 cm in length (Marliave 1977). Intertidal pricklebacks are similar to adult clingfish and remain under the protection of boulders at all phases of the tides, so they may not be very available to predation. In contrast, small intertidal sculpins tend to dart around in shallow water and rely on crypsis when in resting positions.

The most abundant intertidal sculpin is the tidepool sculpin, which is perhaps the most ubiquitous intertidal fish in the Strait of Georgia, occurring on all rocky shorelines. The biology of this species has been documented for open coastal regions with tidepools, where different age-classes occupy pools at different tidal levels (Green 1971). In the strait, similar residence in tidepools is typical where such pools exist. The same species is abundant, however, in fjords such as Indian Arm, where pools are notably lacking. In such areas, the tidepool sculpin tends to strand under rocks at low tide (JBM, pers. obs.). The tidepool sculpin may be a prey of diving ducks. On Popham Island in Howe Sound (Fig. 1), where diving ducks overwinter in abundance, this species tends to function as an annual, with 1-yr-old fish disappearing during their second winter, just prior to the spring spawning period (JBM, pers. obs.). In other areas of the Strait of Georgia, such as Vancouver Harbour, where diving ducks are not typically abundant through the winter, the tidepool sculpin shows several year-classes, as is the case in open coastal areas (Green 1971). The age-classes in the strait are indicated in terms of size frequencies and fecundities (determined from spawned egg masses).

The next most common intertidal sculpin along rocky shores of the Strait of Georgia is the flathead sculpin. The flathead sculpin has broad habitat range, the settling larvae showing no substrate preferences (Marliave 1977). The padded sculpin (*Artedius fenestralis*) typically occurs along with *A. lateralis* but in lower abundance and with deeper depth distribution. These *Artedius* species grow to over 10 cm in length, compared with lengths under 10 cm for the other rocky intertidal sculpins. The manacled sculpin (*Synchirus gilli*) is common on seaweeds in shallow waters having moderate exposure (Miller and Erdman 1948). This species relies entirely on crypsis rather than on hiding under cover. Another small sculpin that tends not to seek cover is the sharpnose sculpin of rocky tidal passes. This species feeds along vertical rock surfaces within a few centimetres of the water line (Lamb and Edgell 1986), and the spawn is deposited under rockweed (*Fucus distichus*) in the high intertidal area (Marliave 1981). Although the distribution is patchy, this species is abundant in certain localities.

The blennioid fishes of the Strait of Georgia include eel-shaped intertidal fishes of two families—the pricklebacks and the gunnels. Although pricklebacks are abundant on rocky shores with boulders and cobble, they remain hidden under rocks and may not be available as prey to seabirds. The cockscomb prickleback is abundant in all exposures and is probably second only to the tidepool sculpin in overall abundance in the strait. In contrast, the two *Xiphister* species occur only on exposed shores. Their secretive habits contrast somewhat with those of the gunnels, which hide in eelgrass and seaweeds and are therefore frequently visible when in motion. The penpoint gunnel usually occurs in eelgrass beds on sandy shores, as well as uncommonly among red and green seaweeds on rocky, cobbled shores of the strait. The two *Pholis* species have distributions somewhat similar to those of the penpoint gunnel, although more restricted to eelgrass habitat; the saddleback gunnel is most frequent on soft bottom near stream outlets (Hart 1973).

On sandflats and mudflats too shallow for eelgrass, arrow gobies, juvenile starry flounders, and juvenile staghorn sculpins are abundant. The arrow gobies occur in the most shallow pools, remaining dispersed near the ghost shrimp burrows in which they take refuge (MacDonald 1975). Juvenile starry flounders rely on crypsis, lying on soft substrate in the open on shallow flats (Orcutt 1950). Juvenile staghorn sculpins prefer tidal streams on shallow flats and, being euryhaline, will extend their distribution well up into estuaries (Jones 1962). These tidal flat species do not have the advantage of a continuous cover of cobble shores, so they are usually visible when in motion.

6.2. Biomass

Biomass of intertidal and shallow subtidal fishes in the Strait of Georgia is unknown, but a rough estimate can be made based on estimated densities for specific situations in Puget Sound. Cross (1981, Table 3) estimated the average standing crop of fishes in rocky headlands as 52.6 g·m^{-2} (SD = 56.6), of which 34.3 (SD = 36.3) were cottids, 16.5 (SD = 25.3) were stichaeids and gunnels, and 1.7 (SD = 3.5) were other fishes. On cobble beaches, the total estimate was 42.0 g·m^{-2} (SD = 50.2), of which 25.6 (SD = 37.8) were cottids, 11.6 (SD = 19.5) were stichaeids and gunnels, and 4.8 (SD = 10.5) were other fishes. Moulton (1977, Table 7) estimated seasonal variation in biomass of fishes in rocky nearshore habitats at two locations in Puget Sound. Estimated mean biomass (g·m^{-2}) and standard error (SE) for all species were 8.1 (SE = 1.6) and 42.2 (SE = 20.3) for the period of January–March; 16.1 (SE = 4.3) and 20.9 (SE = 8.5) for April–June; 22.7 (SE = 3.2) and 42.3 (SE = 23.2) for July–September; and 15.6 (SE = 4.4) and 13.5 (SE = 12.2) for October–December. In both locations, biomass peaked during the summer.

The biomass estimates for nearshore, rocky habitat of Cross (1981)—approximately 50 g·m^{-2}—and Moulton (1977)—about 40 g·m^{-2}—for summer months are roughly similar. Therefore, assuming an estimate of 40 g·m^{-2} as representative of all shallow, rocky areas in the Strait of Georgia, which has a total of about 320 km^2 of such areas (Levings *et al.* 1983), there should be about 13 000 t biomass. This estimate does not include the biomass of intertidal and shallow subtidal fishes inhabiting the 925 km^2 of sand and mud habitat in the Strait of Georgia (i.e., about 82% of the total area between depths of 0 and 20 m). If the same fish densities were found in these areas, then there would be an additional 37 000 t. However, it is probable that fish biomass is higher in rocky areas than in sand and mud areas. For instance, nearly 85% of the total algal biomass found between 0 and 20 m occurs in rocky areas (Levings *et al.* 1983), and many fish tend to associate with submergent algae. If the intertidal fish biomass were distributed in the same way, there would be only about 6000 t of fish in the sand and mud areas. Therefore, total biomass of intertidal and shallow subtidal fishes would be between 20 000 and 50 000 t during the summer months, with lower abundance during winter.

7. Deep-water fishes

There is a group of deep-water fishes that are largely unavailable to birds as prey, but it must be included in this discussion for two reasons:
(1) most fishes have larval or juvenile stages that may be vulnerable to bird predation for short periods, usually in the late spring or early summer; and
(2) deep-water fish in the Strait of Georgia are surprisingly abundant, and any discussion of the fish community within the strait would be incomplete without brief mention of the most important species.

The Pacific hake (*Merluccius productus*) is a deep-water species with at least several resident stocks in the Strait of Georgia. Spawning occurs from March to May. The main spawning area is in the southern strait, south of Halibut Bank (Fig. 1). A smaller stock spawns near Montgomery Bank (Fig. 1), northwest of Texada Island. Pacific hake may be the most abundant fish species in the strait, with a total biomass estimated to be between 85 000 and 130 000 t (McFarlane and Beamish 1985).

The walleye pollock (*Theragra chalcogramma*) is a gadoid with resident stocks within the Strait of Georgia. Total biomass in the strait was estimated at about 23 000 t. Generally, the adults are found in waters deeper than 50 m. Spawning occurs in March and April at depths of 50 m or greater; as larvae develop, they approach the surface layers and may be abundant in shallow waters from February to May, decreasing thereafter and becoming absent after July (Shaw and McFarlane 1986).

Several stocks of Pacific cod (*Gadus macrocephalus*) occur within the Strait of Georgia, including two resident stocks: one that spawns in the vicinity of Nanoose Bay (Fig. 1), another in the Gulf Islands. Two other itinerant stocks occur in the southern Strait of Georgia and Strait of Juan de Fuca (Westrheim and Foucher 1987).

Although not particularly important as a prey species for seabirds, the spiny dogfish (*Squalus acanthias*) is abundant in the Strait of Georgia. Catches in excess of 5000 $t \cdot yr^{-1}$ were taken in the 1940s, with maximum catches approaching 20 000 t. The total biomass of the stock has fluctuated over time, partially as the result of intense fisheries, but it is likely that the total resident biomass is in excess of 100 000 t (Tyler and McFarlane 1985).

8. Conclusions

Some very general conclusions may be made about the fishes of the Strait of Georgia that apply to most regions of the BC coast:
(1) most of the fish species spawn in shallow water;
(2) most of the fish species spawn in the late winter or early spring; and
(3) most of the small species and young stages of larger species appear to spend substantial amounts of time in shallow water where, presumably, they are feeding or avoiding predators.
The consequence to seabird predators is that prey species will become abundant during the spring months mainly in the form of spawning adults, and in the summer as juveniles.

From the discussion and analysis presented above, we make several tentative conclusions that apply specifically to the Strait of Georgia. One is that most of the adult stages of shallow-water pelagic fishes (e.g., salmon, herring, smelts) are migratory and spend relatively little time in the strait. This is significant to the topic of seabird predation, for several reasons. Predators of pelagic fishes, in general, would not have a predictable supply of food every year, as each of the migratory species undergoes substantial fluctuations in abundance, sometimes on a regular time scale (salmon) or on an irregular scale (herring). The circumstances would favour seabirds that are able to feed opportunistically.

Herring are probably the single most important prey species for many, if not most, seabird species. However, most predation would be confined to the juvenile stages, either age 1+ or age 2+ fish, because most of the older age-classes migrate out of the Strait of Georgia following spawning in March and do not return until early winter. Even then, they tend to confine themselves to relatively few deep areas, generally inaccessible to seabirds, until they move into shallow water prior to spawning.

Pacific sandlance is another important prey species, but it is impossible at the present time to make any reasonable estimate of its abundance—except to say that it is abundant relative to other species, so probably its biomass would be measured in the tens of thousands of tonnes.

All *Oncorhynchus* species and the anadromous trouts and chars have juveniles that inhabit parts of the Strait of Georgia prior to moving to the open ocean, where most of their growth occurs. Pacific herring are resident in the strait during three periods: first, as eggs, larvae, and juveniles; then as adults entering the strait to reside in winter holding areas (October–February); and later to spawn (March and April), prior to departing for the offshore waters after spawning. Therefore, most of the herring and salmonids appear to use the strait as a large nursery and rearing area and move to open waters for summer feeding, when most of their feeding and growth occurs.

The Strait of Georgia supports a substantial biomass of resident species, such as hake, pollock, Pacific cod, lingcod, and rockfish. These species are found mainly in deeper waters, but their larval or juvenile stages usually spend time in waters near the surface during the spring and summer and may be vulnerable to seabird predation at that time.

By making some simple generalizations about mean body weight of the dominant species in the Strait of Georgia, one can estimate their approximate biomass. First, herring, by the end of their first summer, usually weigh about 3 g (Hourston 1956; Houde and Berkeley 1982). Total numbers of first-year herring vary from about 0.2 to 3.2 billion (Haist *et al.* 1987), corresponding approximately to a total biomass ranging between 600 and 9600 t, in the poorest and best years, respectively. In the second year, herring weigh about 10 g in the early summer, so total biomass of age 2 herring in the early summer could vary between 1500 and 21 000 t, based on abundances of 0.2–2.1 billion individuals in the poorest and best years, respectively. A rough estimate of juvenile salmonid weight, averaged over all species, is about 10 g (MCH, unpubl. data). Therefore, total numbers for all salmonid species combined vary roughly between about 400 million and 1 billion, corresponding to a total biomass of between 4000 and 10 000 t. The estimated biomass of intertidal species was estimated to vary between 20 000 and 50 000 t. We emphasize that these calculations are crude at best, but they do serve to illustrate the relative abundance and importance of the major groups of fishes as prey for seabirds.

All the intertidal fishes in the Strait of Georgia are year-round residents of the shoreline. They are also small enough at all life stages to constitute prey for birds. Although the total biomass is relatively low when compared with those of the herring, salmonid, and sandlance populations of the strait, the availability of intertidal fishes during midwinter is perhaps unique. Juvenile herring migrate to deeper water in the fall (Taylor 1964). Similarly, salmon smolts migrate to the open ocean before winter. The inshore sandlance of the North Atlantic, *Ammodytes americanus* (considered synonymous with the North Pacific *A. hexapterus* by Richards *et al.* 1963), is subject to a spring/summer commercial fishery, but cannot be caught in winter except with bottom grabs or dredges (Macer 1966). Reay (1970) suggested that sandlance schools move into deep water to overwinter in sand. This species also buries itself in sand at night and during low plankton abundance. Similarly, the most abundant embiotocid in the Strait of Georgia, the shiner perch, occurs in shallow water only from May through October (Gordon 1965). Thus, a major portion of the fish biomass in the strait becomes unavailable to marine birds during the winter, when large aggregations of diving birds congregate there.

The above-mentioned possibility that diving birds at Popham Island may harvest most of the older year-classes of tidepool sculpins during the winter period suggests that further attention be devoted to seasonal availability of fish as prey. Intertidal fishes may provide a small but essential food resource to birds wintering in the Strait of Georgia (Vermeer 1983).

In conclusion, we would like to point out that the incidence of fishes, in terms of their species composition, numbers, and size—as recovered from avian predators—may not necessarily reflect the composition of fish species in nature. Instead, the avian prey selection probably reflects the vulnerability or availability of prey species. There are several reasons why prey fish composition may differ from the composition of the fish community at large. An obvious cause is fishing activities in which some fishes are captured and discarded, or injured and not captured, during the fishing process. One example is the "shaker" mortality caused by the release of small salmonids from hooks. Fish released in this way would be disoriented and close to the surface and therefore especially vulnerable to avian predators. There also are injured fish resulting from the herring roe fishery, in which an estimated 1% of the catch is "lost" by falling overboard before the nets can be hauled aboard vessels (Hay *et al.* 1982). This loss is quite low relative to other fishing activities, but nevertheless there may be up to 100 t of herring (about 600 000 individual spawning fish) lost during the annual roe fishery in the Strait of Georgia. Another example caused by human activity could be small, localized fish kills (often juvenile herring overcome by localized anoxia) associated with spills at industrial plants (DEH, pers. obs.; J. Morrison, Department of Fisheries and Oceans, Nanaimo, BC, pers. commun.). It is likely that such situations are feeding opportunities for some species.

There are also at least several natural situations that could lead to unusual prey taken by birds. For unknown reasons, anchovies sometimes attempt to swim up rivers such as the Serpentine River (Fig. 1), which drains into Boundary Bay. Anchovies are intolerant of prolonged exposure to fresh water and die. Another example is the annual Fraser River freshet, which flushes some normally freshwater species into the Strait of Georgia. During a fishing expedition for surf smelt on sandy beaches near Spanish Banks (Fig. 1), some peamouth chub (*Ptychocheilus oregonensis*) were taken in addition to the smelt (DEH, pers. obs.). Also, Barraclough and Robinson (1971), while fishing in the spring months at the time of the Fraser River freshet, found juvenile freshwater carp (*Cyprinus carpio*), a Eurasian import that lives in the lower Fraser River, in several locations in the southern Gulf Islands. These carp probably could not tolerate the higher salinities that develop in the summer and therefore would probably be taken by predators.

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Aquatic plant resources of the Strait of Georgia

Ian Hutchinson, Alison Campbell Prentice, and Gary Bradfield

1. Abstract

Aquatic plants of intertidal and shallow subtidal habitats in the Strait of Georgia form the base of the food chain that supports the large migratory waterfowl populations. The main plants eaten by birds are sedges (*Carex*), bulrush (*Scirpus*), ditch-grass (*Ruppia*), eelgrass (*Zostera*), and some algae (mainly *Ulva* and *Enteromorpha*).

The tidal marshes of the Strait of Georgia may be classified by salinity and geographic criteria into three general types:
(1) saline marshes, which occur mainly along the east coast of Vancouver Island and in Boundary Bay;
(2) brackish marshes, which occur at the mouths of the large rivers; and
(3) fjord-head marshes, found only along the mainland coast of the strait.
The nature and distribution of the plant communities of these marsh types are described, and the standing crops and seed production values of the plants utilized by birds are documented.

The nature and regional distribution of eelgrass, ditch-grass, and macroalgal communities are described, and the environmental conditions associated with the presence of the communities are examined. Available data on standing crop, productivity, and relative utilization of these communities by the waterfowl of the region are also given.

Of the 4450 ha of intertidal marsh habitat in the Strait of Georgia at the time of European settlement, one-third was alienated by the end of the 19th century as a result of agricultural diking. Losses of intertidal marsh habitats since that time have been exceeded by additions as a result of marsh progradation. There are currently some 3650 ha of intertidal marsh in the strait, almost 80% in the Fraser River estuary. The pattern of areal losses and gains has not been uniform; conversion was most extensive on the intermediate and larger deltas, and progradation has been most rapid on the deltas with the largest sediment supply.

In addition to areal change, wetland communities in the Strait of Georgia have undergone successional change as a result of aggradation of the marsh platform. The deltaic platforms of the larger rivers, which support nonsaline marshes, aggrade rapidly, and the rates of successional turnover in these marshes are estimated to be an order of magnitude greater than those of the smaller, saline marsh deltas.

2. Résumé

Les plantes aquatiques des habitats intertidaux et infralittoraux peu profonds du détroit de Georgia constituent la base du réseau alimentaire qui fait vivre les grandes populations d'oiseaux aquatiques migrateurs. Les principales plantes dont se nourrissent les oiseaux sont les laîches (*Carex*), les quenouilles (*Scirpus*), la ruppie (*Ruppia*), la zostère (*Zostera*) et quelques algues (surtout *Ulva* et *Enteromorpha*).

Les marais littoraux du détroit de Georgia peuvent être classés, selon leur salinité et leurs caractéristiques géographiques, en trois types généraux :
(1) les marais salins, qui se trouvent surtout sur la côte est de l'île de Vancouver et dans la baie Boundary;
(2) les marais saumâtres, à l'embouchure des grands cours d'eau;
(3) les marais au fond de fjords, qui se trouvent seulement sur la côte continentale du détroit.
La nature et la distribution des associations de plantes vivant dans ces types de marais sont décrites, des données sont présentées sur la biomasse des plantes dont se nourrissent les oiseaux, et des chiffres sont fournis sur la production de graines par ces plantes.

La nature et la distribution régionale des communautés de zostères, de ruppies et d'algues macroscopiques sont décrites, et les conditions environnementales associées à la présence de ces communautés sont étudiées. On fournit également les données disponibles sur la biomasse et la productivité de ces communautés de même que sur leur utilisation par les oiseaux aquatiques.

Des 4450 ha de marais intertidaux du détroit de Georgia qui servaient d'habitats lors de la colonisation par les Européens, un tiers a été perdu à la fin du XIX^{e} siècle en raison de la construction de digues à des fins agricoles. Depuis ce temps, les ajouts ont été supérieurs aux pertes à cause de la progradation des marais. Il existe actuellement 3650 ha de marais intertidaux dans le détroit, dont 80 % se trouvent dans l'estuaire de fleuve Fraser. Le régime des pertes et des gains de superficie n'a pas été uniforme; la conversion a été la plus considérable dans les deltas intermédiaires et les grands deltas, et la progradation a été la plus rapide dans les deltas où il y a le plus de sédiments.

En plus des changements de superficie, les milieux humides du détroit de Georgia ont subi des changements évolutifs en raison de l'alluvionnement de la plate-forme des marais. La plate-forme du delta des grands cours d'eau, où l'on trouve des marais non salins, s'alluvionne rapidement, et, dans ces marais, le taux de changement

évolutif est dix fois plus grand que celui des petits deltas où l'on trouve des marais salins.

3. Introduction

Many of the bird species that occur in the Strait of Georgia are dependent on its aquatic plant resources: intertidal and subtidal plant communities provide not only food but also cover, nesting habitat, and roosting sites (Verbeek and Butler, this publication). In this paper, we focus on aquatic plants as sources of food or as components in the estuarine food chains of which birds are a part.

The intertidal and shallow subtidal vascular plant and algal communities of the Strait of Georgia serve as food sources for birds in several ways (Fig. 1). Relatively few studies of the dietary habits of the herbivorous birds of the Strait of Georgia have been undertaken (Burgess 1970; Burton 1977; McKelvey 1981; Eamer 1985). These studies, and those from elsewhere in western North America (Martin *et al.* 1951; Yocom 1951), have demonstrated that the preferred food items are intertidal marsh plants (particularly the sedge genera *Scirpus* and *Carex*), eelgrass (*Zostera*), ditch-grass (*Ruppia*), and algae (especially *Enteromorpha* and *Ulva*) (Fig. 2). Our discussion focuses on the distribution, abundance, productivity, and environmental conditions associated with these genera in the Strait of Georgia.

Section 4 of this paper outlines a classification of the intertidal marshes based on salinity and geomorphic criteria. The three main marsh types recognized (saline, brackish, fjord-head) are illustrated by specific examples. When available, data on the productivity of the major marsh plants eaten by birds are presented. A potential connection between Snow Geese (*Chen caerulescens*) grubbing, geomorphic processes, and plant community dynamics in brackish, foreshore marshes is highlighted in Section 4.2.1. Section 5 discusses eelgrass, ditch-grass, and macroalgae as important avian food plants of intertidal channels and ponds and shallow, subtidal mudflats. Section 6 addresses the dynamic nature of intertidal and subtidal ecosystems, particularly marshes. Data are presented on the changes in areal extent of these habitats that have occurred in the Strait of Georgia since the 1860s.

4. Intertidal marshes

Intertidal marshes are developed on the foreshores of deltas along the relatively exposed portions of the coast of the Strait of Georgia, in confined fjord-heads, or in embayments behind barrier bars and spits. The locations of all intertidal marshes more than 10 ha in area are shown in Figure 3; Figure 4 presents data on the relative abundance of waterfowl food plants in each marsh.

4.1. Saline marshes

Hutchinson (1988) described the intertidal marshes of the Puget Trough lowlands (including the Strait of Georgia) in terms of their locations along an estuarine salinity gradient. At the saline pole of this gradient is a group of relatively small intertidal marshes that are associated with open-coast deltas or bays where there is limited freshwater inflow and/or strong maritime

Figure 1
Generalized food web of a Strait of Georgia marsh. Compartments and pathways relating specifically to birds are highlighted. All flows are from bottom to top except where noted (modified from Long and Mason 1983).

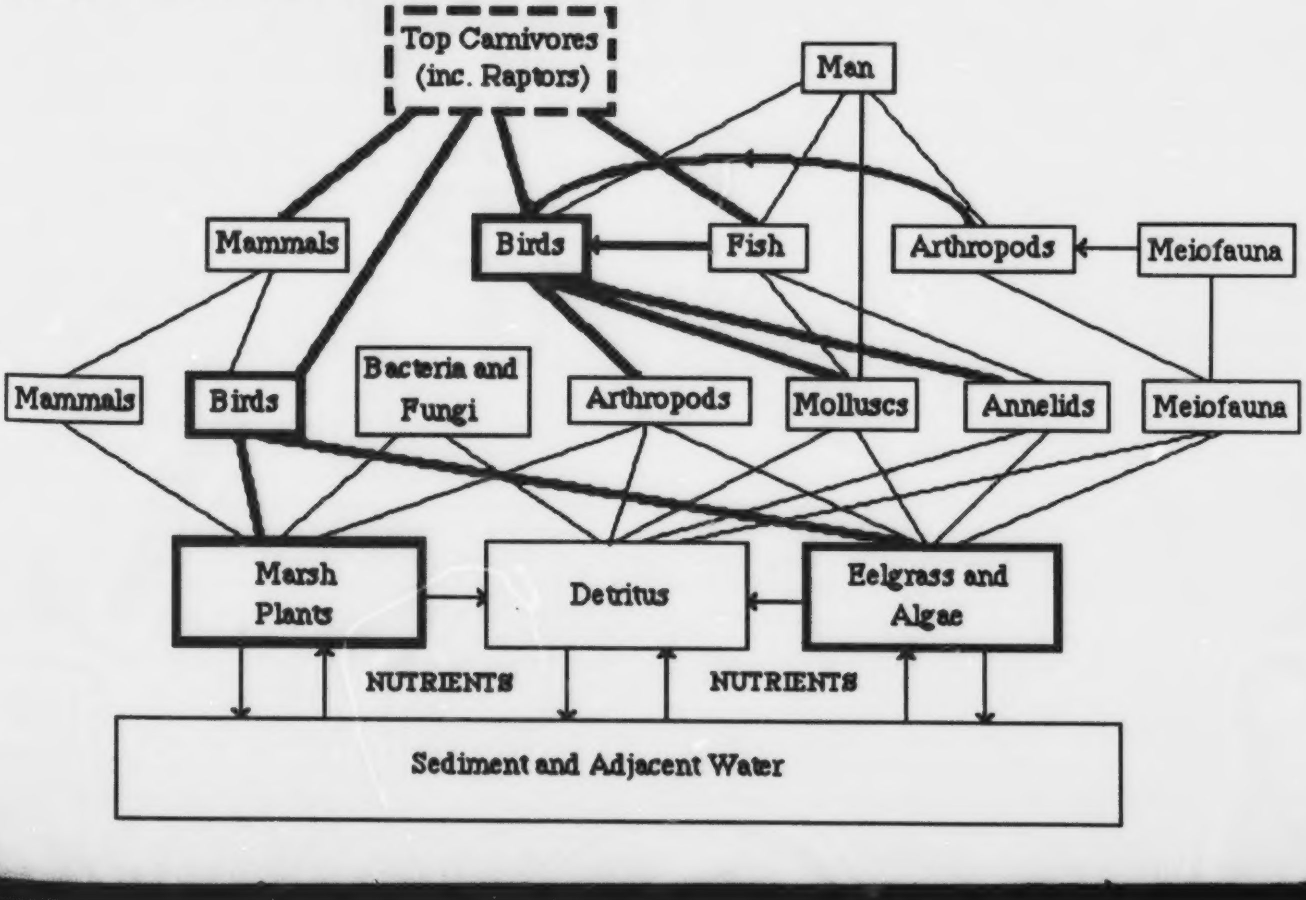


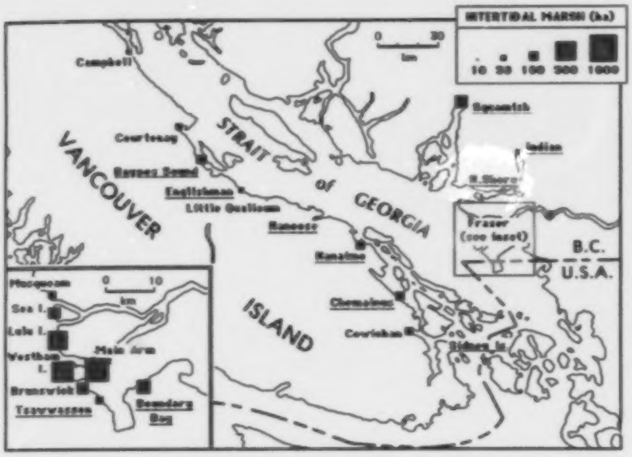
Figure 2
Wild plant food preferences of the common herbivorous waterfowl and rails of the Strait of Georgia. Only those birds with a diet consisting of >50% plant matter at any time of the year are included.

PLANTS BIRDS	Algae	Atriplex	Carex	Distichlis	Eleocharis	Menyanthes	Ruppia	Sagittaria	Scirpus	Triglochin	Typha	Zostera	Source
Trumpeter Swan			■						■			■	McK
Canada Goose									■				MZN
Brant	░											■	MZN
Snow Goose			▦						■				Bn
Mallard	▒	▒	■			▒	░	■	■	░			Bs
Northern Pintail	░	░	■				▒		■	░		░	Bs
Green-winged Teal		░	▦		▒	▒			■	░	▒		Bs
Blue-winged Teal			▒	▒	▒		▦		■				MZN
American Wigeon	▦		░				■		░	░		▦	Bs
Northern Shoveler	▒		▒	▦	▦		▒		▦				MZN
Wood Duck					■				■				Y
Redhead	▒		░	░	░		▒		■				MZN
Ring-necked Duck	░		▒				▒		▒				MZN
Canvasback			░				▒						MZN
Greater Scaup							▒	▒	▒				MZN
Lesser Scaup			░		░		▦		▦				MZN
Ruddy Duck			░		░		▦		▦				MZN
Sora Rail	░		■	░					■				MZN
American Coot	▦				░		▒		■				MZN
Median use (all birds)			░				▒		■				
Total no. of users	9	3	14	4	8	2	12	2	17	4	1	4	

Note: Diet (%): ■ >50; ■ 25-50; ■ 10-25; ▦ 5-10; ▒ 2-5; ░ 0.5-2

Sources: Bn=Burton (1977); Bs=Burgess (1970); MZN= Martin et al. (1951);
McK=McKelvey (1981); Y=Yocom (1951)

Figure 3
Location and area of intertidal marshes more than 10 ha in extent in the Strait of Georgia. Names with a solid underline are saline marshes; non-underlined names indicate brackish or freshwater marshes; and dotted underlines indicate fjord-head marshes (from Environment Canada 1975; Romaine *et al.* 1976; Campbell Prentice and Boyd 1988; Hutchinson 1988; R.W. Butler, pers. commun.).

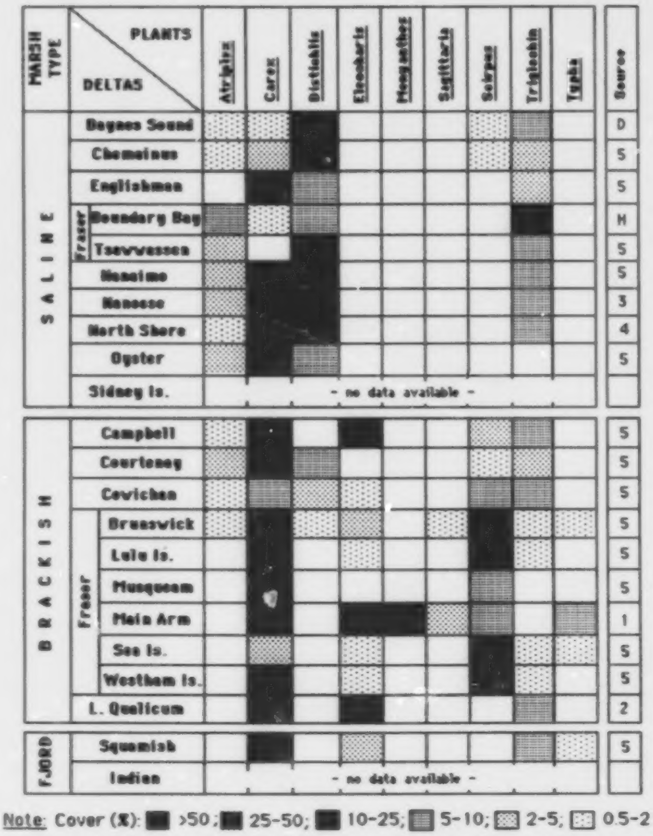


influence. Most of the rivers flowing into these deltas/estuaries have a winter discharge peak that is in phase with the local precipitation regime but out of phase with the growing season. The estuarine waters and marsh substrates therefore tend to be saline in summer and brackish in winter. The marsh vegetation of these deltas consists of a halophytic flora, the relative dominance of which depends upon the runoff regime of the proximate river. In these deltas, plant species characteristic of brackish environments are restricted to river channel margins and outlets.

The Nanaimo River delta marsh is fairly typical of the saline marsh group. The flow of the Nanaimo River at its mouth peaks in December at 80 $m^3 \cdot s^{-1}$, stabilizes at about 40 $m^3 \cdot s^{-1}$ in March–May, and thereafter declines to a minimum of 4 $m^3 \cdot s^{-1}$ in August. The salinity of the marsh and tidal flat is therefore lowest when plant growth is initiated in early spring and rises to a peak in late summer, when high evapotranspiration rates may induce hypersaline conditions at the soil surface in the high marsh (Kask and Sibert 1976; Smythe 1987).

Along most of the delta front the marsh descends to an elevation of about 340–350 cm above chart datum on the deltaic platform, and the low marsh is submerged for approximately 40% of the time (Fig. 5*a*). The low marshes are small in extent and consist of open stands of pickleweed (*Salicornia virginica* L.), arrowgrass (*Triglochin maritimum* L.), saltwort (*Glaux maritima* L.), seaspurry (*Spergularia canadensis* [Pers.] G. Don), and rockweed (*Fucus distichus* [de la Pyle] Pow.). Rockweed is common only in the low marsh, where pebbles occur in the marsh substrate. Close to the main Nanaimo River distributary, the marsh progrades to somewhat lower elevations, where extensive and vigorous stands of Lyngbye's or sea sedge (*Carex lyngbyei* Hornem.) may be found. Species indicative of freshwater conditions are either absent or highly localized in their distribution. Apart from *C. lyngbyei*, sedges are entirely absent, with the exception of the salt-tolerant sea bulrush (*Scirpus maritimus* L.). Stands of the latter species cover only a few square metres on the floors of small tidal channels near the main river distributary.

Figure 4
Relative percent cover of waterfowl food plants in the intertidal marshes of the Strait of Georgia



Note: Cover (%): ■ >50; ■ 25-50; ■ 10-25; ▤ 5-10; ▒ 2-5; ░ 0.5-2

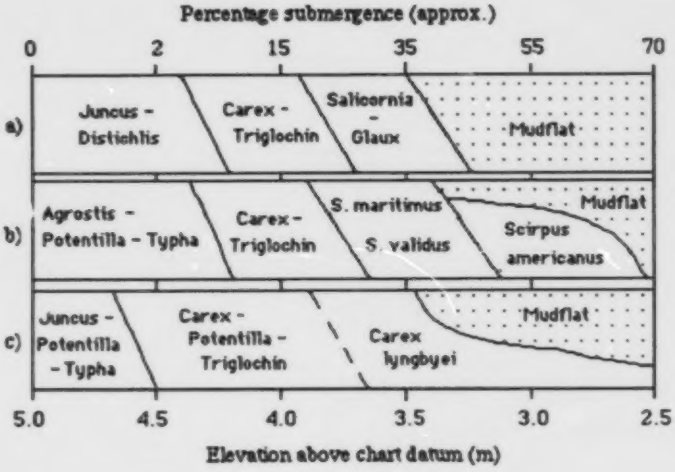
Sources: (1) Bradfield and Porter (1982); (2) Dawe and White (1982); (3) Dawe and White (1986); (4) Environment Canada (1975); (5) Hutchinson (1982); (6) Hutchinson (1988); (D) N.K. Dawe, unpubl. data; (H) I. Hutchinson, unpubl. data.

High-marsh communities on the Nanaimo River delta consist of clonal mosaics of *C. lyngbyei*, saltgrass (*Distichlis spicata* [L.] Greene), and rushes (*Juncus balticus* Willd.; *J. gerardii* Loisel.), with an admixture of *Salicornia virginica*, wild barley (*Hordeum* spp.), and *T. maritimum*. Orache (*Atriplex patula* L.), an annual, is characteristic of disturbed sites and wrack deposits associated with high-tide drift-lines. *Carex lyngbyei* is particularly common along the margins of tidal channels; the plants in these habitats are usually taller and more vigorous than those in the high-marsh meadows. The upper meadows are submerged for less than 5% of the time; most areas are virtually supratidal. The substrates in the high marsh are dominantly organic; fine-grained muds occur in the tidal channels.

Standing crops (= above-ground biomass) in the high marsh are about 600–800 $g \cdot m^{-2}$ (Hutchinson 1986). The saline low-marsh communities are usually fairly open, and standing crops are generally less than 300 $g \cdot m^{-2}$. Channel-margin stands of *C. lyngbyei* usually have standing crops exceeding 1000 $g \cdot m^{-2}$.

The low influx of fresh water effectively inhibits the establishment of *Scirpus* and *Eleocharis*. Utilization of the marsh by waterfowl for feeding is therefore mainly limited to the river- and channel-side stands of *C. lyngbyei*. Seed production by this species in these habitats is only a fraction of that of freshwater populations (ca. 24 000 seeds m^{-2}), and the seeds have low (< 15%) viability

Figure 5
Vertical distribution of plant associations in selected intertidal marshes in the Strait of Georgia: (*a*) a saline marsh (Nanaimo River delta); (*b*) a brackish marsh (Lulu Island, Fraser River delta); and (*c*) a fjord-head marsh (Squamish River delta) (from Hutchinson 1982, unpubl. data)



(Smythe 1987). Very few of the *C. lyngbyei* shoots in the high-marsh meadows flower.

One of the few areas of intertidal marsh in the Strait of Georgia that is not in an area of active deltaic sedimentation is the marsh that fringes Boundary Bay on the inactive southern flank of the Fraser River delta. This embayment receives only very limited freshwater flow from the Serpentine and Nicomekl rivers at its eastern end, and the fringing marsh is therefore strongly halophytic in character. The low-marsh associations here consist mainly of *T. maritimum* and *S. virginica; D. spicata* and *S. virginica* are dominant elements in a diverse, high-marsh flora. *Carex lyngbyei* rarely occurs in this saline marsh.

Although annual species of *Salicornia* are known to provide food for dabbling ducks elsewhere (N. Foote, pers. commun.), the perennial *S. virginica* is not an important element in the diet of waterfowl in the Strait of Georgia; however, Eamer (1985) found that both Mallard (*Anas platyrhynchos*) and American Wigeon (*A. americana*) made some use of this species. Feeding in the low marsh is therefore probably restricted to grazing on the young shoots of *T. maritimum* in spring. With the exception of the channel-side stands of *C. lyngbyei*, waterfowl use of the high marsh for feeding is mainly limited to periods of high tides (Eamer 1985).

4.2. Brackish marshes

At the other extreme of the salinity gradient in the Strait of Georgia is a series of open-coast deltas and estuarine embayments in which riverine influences are dominant over maritime influences in the growing season. The rivers associated with the largest of these deltas are to a considerable extent fed by snow- and icemelt, and river flow is consequently at its peak during spring or early summer. Smaller rivers in the brackish marsh group (e.g., the Cowichan River) have two periods of high runoff: a midwinter peak generated by the annual precipitation maximum, and a secondary period of high discharge in late spring and early summer resulting from snowmelt. The water in the estuaries of these rivers is consequently only slightly saline during the early part of the growing season, and the intertidal marsh vegetation is dominated by sedges (*Carex* and *Scirpus* spp.).

The Fraser River delta is the largest member of the brackish marsh group in the Puget Trough. More than 80% of the flow of this river is concentrated in the period between May and July, and the salinity in most of the foreshore marsh substrate declines from about 15–20% in winter to less than 5% in summer (Karagatzides 1987; IH, unpubl. data). As with their saline counterparts, these brackish marshes usually develop a simple zonation into low and high marsh, although in some instances a transitional middle marsh may be recognized (Fig. 5*b*). The low-marsh community consists of common three-square bulrush (*Scirpus americanus* Pers.) and sea bulrush (*S. maritimus*). *Scirpus americanus* usually forms the leading edge of the marsh, colonizing relatively well-drained sandy silts down to 260–300 cm above chart datum. These stands are submerged some 50% of the time. *Scirpus maritimus* is restricted to anoxic muds and is dominant along the edges and beds of small tidal creeks or ponds. The high marsh is dominated at its leading edge by *C. lyngbyei* and *T. maritimum* (= the middle marsh of some authors). In areas close to distributaries, this zone is backed by stands of cattail (*Typha latifolia* L.) and tule (*Scirpus validus* Vahl.), separated by meadows of *C. lyngbyei*, bentgrass (*Agrostis alba* L.), and Pacific silverweed (*Potentilla pacifica* Howell). In more saline interdistributary areas, *C. lyngbyei, Deschampsia cespitosa* (L.) Beauv., and *D. spicata* are prominent. Smaller deltas of the brackish marsh group (e.g., the Cowichan River delta) have large areas of this type of high marsh on the foreshore and much smaller expanses of *Scirpus* low marsh. Some low-marsh areas distant from freshwater influence may be dominated by *S. virginica, S. canadensis,* and *G. maritima*.

The distributary-margin deposits and within-channel islands of the larger deltas of the Strait of Georgia commonly support expanses of intertidal marsh (e.g., Ladner and the Island Complex marshes in the Fraser River delta, Campbell River delta). Tidal saltwater intrusion into these estuaries is usually limited, and the marsh floras are consequently dominated by freshwater elements. At Ladner marsh in the Fraser River delta, for example, Bradfield and Porter (1982) recognized three plant associations, dominated by *C. lyngbyei*, tall fescue (*Festuca arundinacea* Schreb.), and buck bean (*Menyanthes trifoliata* L.).

The mean total biomass (above and below ground) in the low sedge marshes on the Fraser River delta foreshore amounts to 880–2300 $g \cdot m^{-2}$ (*S. americanus*) and 3200–12 000 $g \cdot m^{-2}$ (*S. maritimus*) (Karagatzides 1987). The peak standing crop of these low-marsh species in the Pacific Northwest ranges in general from 300–600 $g \cdot m^{-2}$ (*S. americanus*) to 550–1000 $g \cdot m^{-2}$ (*S. maritimus*) (Karagatzides 1987). Values at the higher end of this range tend to be associated with isolated clones in middle- or high-marsh sites. Standing crops in the high marsh are quite variable. In the grassy meadows dominated by *A. alba*, typical peak standing crop values are about 500 $g \cdot m^{-2}$, rising to 700–900 $g \cdot m^{-2}$ if *C. lyngbyei* or *Juncus balticus* Willd. is present. Stands of *S. validus* have similar standing crop values. The largest standing crops in these marshes are associated with dense stands of *T. latifolia*, which commonly attain peak values between 1500 and 2000 $g \cdot m^{-2}$ (Hutchinson 1986).

The seeds of the brackish marsh sedges form one of the most important components in the diet of dabbling ducks in the Strait of Georgia (Burgess 1970). Karagatzides (1987) reported that some 66% of the low-marsh *S. americanus* shoots produce flowers, compared with 83% in the high marsh, and Burgess (1970) noted a mean production of 14 seeds per shoot in the Fraser River populations. Given a mean density of 1400 shoots per square metre at the leading marsh edge and 3500 shoots per square metre at the upper elevational limit for this species (Karagatzides 1987), we estimate that mean seed production ranges between 13 000 and 41 000 seeds per square metre. Using a similar metric, we estimate seed production in the case of *S. maritimus* to be very low (<2000 seeds m^{-2}). For the sake of comparison, *C. lyngbyei* produces about 100 000 seeds per square metre in the Fraser River foreshore marshes (S.R. Smythe, pers. commun.).

4.2.1. *Snow Goose use of brackish marshes*

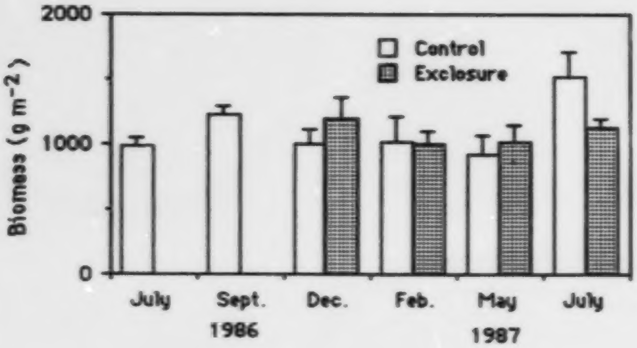
The most prominent herbivore in the *Scirpus* communities of the Fraser River delta (and the neighbouring Skagit and Stillaguamish deltas in the state of Washington) is the Snow Goose. The large overwintering flocks of this species in the Puget Trough, commonly consisting of 10 000 to 20 000 birds (but at times reaching 50 000), may play an important role in marsh community dynamics. The geese are present from October to April, and their major energy sources during this period are the rhizomes of *S. americanus* and, to a much lesser extent, the corms and rhizomes of *S. maritimus* (Burton 1977). During the winter months, tides and waves remove all above-ground material from the *S. americanus* stands; only the bases of shoots remain in *S. maritimus*. The geese grub in these virtually bare marsh muds for the rhizomes and corms that constitute the storage reserves for shoot initiation in the spring. On the basis of a feeding experiment with captive geese, Burton (1977) concluded that some 32% of the total below-ground biomass of *S. americanus* was removed each winter by the Snow Geese flocks. However, exclosure experiments on the Sea Island portion of the Fraser River delta foreshore (IH, unpubl. data) showed no significant difference in total below-ground biomass of *S. americanus* between areas in which grubbing was taking place and the areas from which the geese had been excluded (Fig. 6).

Although Snow Geese may not lower the underground reserves of *S. americanus* significantly in a single winter, in the long term they produce marked changes in the microtopography (and possibly the sedimentation pattern) of the low marsh. Their grubbing creates craters in the marsh surface. The water that remains in these craters at low tide provides refuge habitat for waterfowl and juvenile fish. The sediment released by the feeding activity of the geese (which usually takes place on a flooding tide) is deposited at higher elevations on the marsh platform. The extensive sheets of soft mud that lie upmarsh from the *S. americanus* zone and that produce the anoxic substrates on which *S. maritimus* is dominant may thus be an indirect effect of Snow Goose feeding.

For a month or so prior to their departure in spring, the geese feed on the elongating shoots of *C. lyngbyei*; at this time of year, the high-marsh drift-lines consist almost entirely of the tough sheaths of *C. lyngbyei* shoots discarded by the birds. Sean Boyd (Can. Wildl. Serv.) is currently beginning a research program aimed at investigating the effects of the geese on the dynamics and organization of the plant communities of the Fraser River and Skagit River deltas.

In brackish deltaic marshes where Snow Geese are absent, Trumpeter Swans (*Cygnus buccinator*) may perform a similar ecological role. Their large feeding craters are a common feature of the *S. americanus* zone of the deltas of the Cowichan, Courtenay, and Somass rivers on Vancouver Island (McKelvey 1981; Lee and McKelvey 1984), and they have also been observed feeding in *Carex* communities in the Little Qualicum River (N. Dawe, pers. commun.) and Nanaimo River (IH, pers. obs.) estuaries.

Figure 6
Mean (± SE) total biomass (above and below ground) in low-marsh stands of *Scirpus americanus* on the foreshore of Sea Island, Fraser River delta, subjected to Snow Geese grubbing (controls), and in seven 10-m^2 exclosures established in October 1986 (from IH, unpubl. data)



4.3. Fjord-head marshes

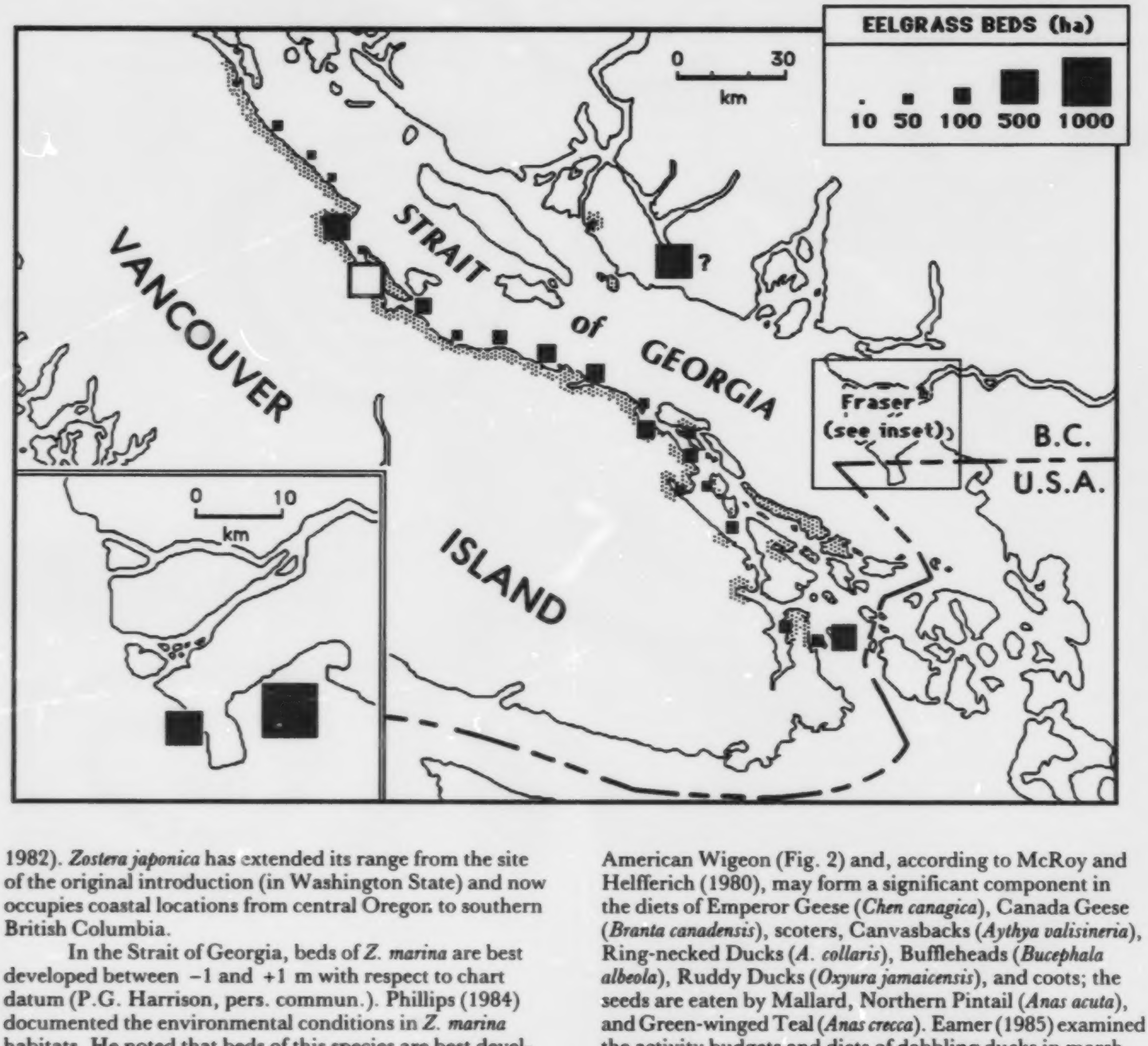
The marshes of the fjord-head deltas of the Strait of Georgia (and the remainder of the mainland coast of British Columbia), with the exception of the Squamish River, have received very little scientific attention. In the case of the Squamish River, the intertidal marsh consists of large expanses of virtually monospecific stands of *C. lyngbyei*, with an admixture of rockweed in the more saline, low-marsh areas, and *T. maritimum* and *P. pacifica* in the intermediate marsh (Fig. 5*c*). The high marsh consists of a diverse mix of freshwater wetland (e.g., *Typha*) and wet meadow species close to the main river channel, and stands of *Deschampsia* in more saline locations. The high marsh grades into willow scrub and floodplain spruce-cottonwood forest. The meagre descriptions of fjord-head marsh plant communities elsewhere along the coast of British Columbia (Levings *et al.* 1975) indicate that they conform to the Squamish model.

5. Eelgrass, ditch-grass, and macroalgae

5.1. Eelgrass

Two species of eelgrass occur in our coastal waters. *Zostera marina* L. is a widespread native perennial that grows in the low intertidal and the shallow subtidal zones on gently sloping, fine-textured coastal deposits in sheltered situations. For this reason, the *Z. marina* beds in the Strait of Georgia are essentially limited to the extensive areas of this habitat type along the east coast of Vancouver Island and on the flanks of the Fraser River delta (Fig. 7). The rocky, steeply sloping coastline of the mainland of British Columbia offers few available habitats for eelgrass colonization. *Zostera japonica* Aschers & Graebn. is an introduced species with a much more restricted distribution in the strait at present. The seeds of this annual (or short-lived perennial) species were likely imported in shipments of oyster spat from Japan in the early decades of the present century (Harrison 1976; Harrison and Bigley

Figure 7
Areal extent of eelgrass (*Zostera*) beds in the Strait of Georgia. The solid rectangles indicate areas in which eelgrass is dominant; open rectangles indicate a substantial admixture of macroalgae in the eelgrass community. Rectangles are centred on stretches of the coastline that possess eelgrass beds more than 10 ha in extent (from Romaine *et al.* 1976, 1981, 1983).



1982). *Zostera japonica* has extended its range from the site of the original introduction (in Washington State) and now occupies coastal locations from central Oregon to southern British Columbia.

In the Strait of Georgia, beds of *Z. marina* are best developed between −1 and +1 m with respect to chart datum (P.G. Harrison, pers. commun.). Phillips (1984) documented the environmental conditions in *Z. marina* habitats. He noted that beds of this species are best developed where current velocities and wave energies are low and cites an elevational range of −6.6 to +1.8 m for the species in US coastal waters. The rhizomes of this species are incapable of vertical growth, thus limiting the development and tenure of eelgrass in areas where rapid sediment accretion is occurring. Factors correlated with eelgrass productivity include light levels, temperature regimes, nutrient availability, and carbon supply. *Zostera japonica* is found at higher elevations in the intertidal zone than *Z. marina*. At these elevations, it primarily occupies the beds of small channels that carry water at virtually all states of the tide.

Bird use of eelgrass beds is substantial: the leaves are a major item in the diets of migrating and overwintering flocks of Trumpeter Swans, Brant (*Branta bernicla*), and American Wigeon (Fig. 2) and, according to McRoy and Helfferich (1980), may form a significant component in the diets of Emperor Geese (*Chen canagica*), Canada Geese (*Branta canadensis*), scoters, Canvasbacks (*Aythya valisineria*), Ring-necked Ducks (*A. collaris*), Buffleheads (*Bucephala albeola*), Ruddy Ducks (*Oxyura jamaicensis*), and coots; the seeds are eaten by Mallard, Northern Pintail (*Anas acuta*), and Green-winged Teal (*Anas crecca*). Eamer (1985) examined the activity budgets and diets of dabbling ducks in marsh and mudflat habitats along the east coast of Vancouver Island (from the Little Qualicum River estuary south to Nanoose Harbour) in the winters of 1980 and 1981. Her data indicated that Mallards and American Wigeon spent 50–100% more time feeding in the intertidal marine zone (e.g., tidal pools, tidal channel margins) than in marshes. The diets of these two species (when weighted by duck activity budgets and sample size) comprised 21 and 4% *Zostera* for Mallards and American Wigeon, respectively. In contrast, Burgess (1970) concluded that the seeds of intertidal sedges constituted the major fall and winter food source (Fig. 2), on the basis of an examination of the gut contents of these (and other) hunter-killed dabbling duck species on the Fraser River delta. The discrepancy in these results may be merely a result of different sampling and processing procedures, but it may also indicate that these waterfowl have opportunistic diets. The diet of such "generalist" herbivores commonly reflects resource availability in the locality or seasonal variation in the palatability and nutritional value of the plants (Buchsbaum and Valiela 1987).

Many shorebirds and some ducks feed on the epiphytic fauna associated with eelgrass beds. Herring eggs deposited on eelgrass leaves in the late winter and early spring (Hay *et al.*, this publication) provide food for a wide variety of bird species (Bayer 1980). Birds are likely the most important herbivores in the eelgrass ecosystem. McRoy (1966) estimated that Brant in Alaska consume 180 g dry weight of eelgrass per bird daily. The effects of avian herbivory on eelgrass productivity, nutrient cycling, and stand dynamics have not yet been examined along the Pacific littoral.

The rapid spread of eelgrass "wasting-disease" in the North Atlantic in the 1930s led to drastic declines in the populations of dependent bird species such as Brant, and surviving populations changed their migration patterns and feeding habits. Along the Pacific Flyway, overwintering populations of Brant have remained fairly stable in recent years, but the main populations now winter farther south, possibly as a result of deterioration in eelgrass habitat or industrial and recreational development along the Canadian and US coastline (Reiger 1982*a*, 1982*b*; A. Reed, pers. commun.).

5.2. Ditch-grass

Ditch- or widgeon-grass (*Ruppia maritima*) is an aquatic herb of brackish to saline waters, primarily found in channels and pans in the intertidal marshes of the Strait of Georgia. It is intolerant of prolonged periods of aerial exposure, and seed and shoot production increases with length of submergence (Bigley 1981). *Ruppia maritima* is of prime importance to wildlife, particularly in saline habitats: it provides food and cover for fish; rails eat seeds and shoots; and waterfowl graze on all parts of the plant, including rootstocks (Warrington 1980).

5.3. Macroalgae

There is an extensive database on the areal extent, community organization, and productivity of intertidal and subtidal algal beds in the Strait of Georgia (R. Foreman, pers. commun.). The two most important genera of macroalgae in terms of avian food sources are *Enteromorpha* and *Ulva*. The several species of *Enteromorpha* grow attached to rocks in the upper intertidal zone, epiphytically, or as unattached mats in tidal pools. *Enteromorpha* is tolerant of low salinities and is therefore the primary component of the macroalgal community in some estuarine habitats. Its widespread occurrence is due mainly to its tolerance of a wide range of light intensities, temperature regimes, salinity, and pollution (Waaland 1977). Thom (1981) estimated Net Annual Primary Productivity for *Enteromorpha* species to range from 96 g C m^{-2} (thallus area) for *E. linza* L. J. Ag. to 1296 g C m^{-2} (thallus area) for *E. clathrata* (Roth) Grev. in Gray's Harbor, Washington. He noted that the latter production value is at least three times greater than that reported from benthic algal ecosystems elsewhere.

The other major genus of green alga in the intertidal zone is sea lettuce (primarily *Ulva expansa* [Setch.] S. & G. and *U. fenestrata* P. & R.). It also occurs as attached or free-floating plants in quiet embayments, in tidal pools, and on mudflats. The morphology and anatomy of the genus are variable and change with geographic location, season, water and air temperature, wave exposure, and intertidal position (Tanner 1979).

According to Figure 2, almost half the herbivorous bird species in the Strait of Georgia will feed on macroalgae, but this is a minor component of the diet of most species, with the exception of American Wigeon and coot. As with eelgrass, the relative availability of macroalgae versus other food sources determines the intensity of use. The data provided by Eamer (1985) indicate that 75% of the diet of American Wigeon in her study area consists of green algae (*Enteromorpha* plus *Ulva* = 47%; filamentous algae = 28%), and these algal beds are likely of critical importance for some overwintering populations of waterfowl in the Strait of Georgia. Naiman and Sibert (1979) investigated the sources of organic carbon in the Nanaimo River estuary and concluded that benthic macroalgae were a relatively minor source. Annually, macroalgae produced 0.9–7.5 g C m^{-2}, compared with 4–55 g C m^{-2} for benthic microalgae, 27 g C m^{-2} for eelgrass, and 564 g C m^{-2} for *C. lyngbyei*.

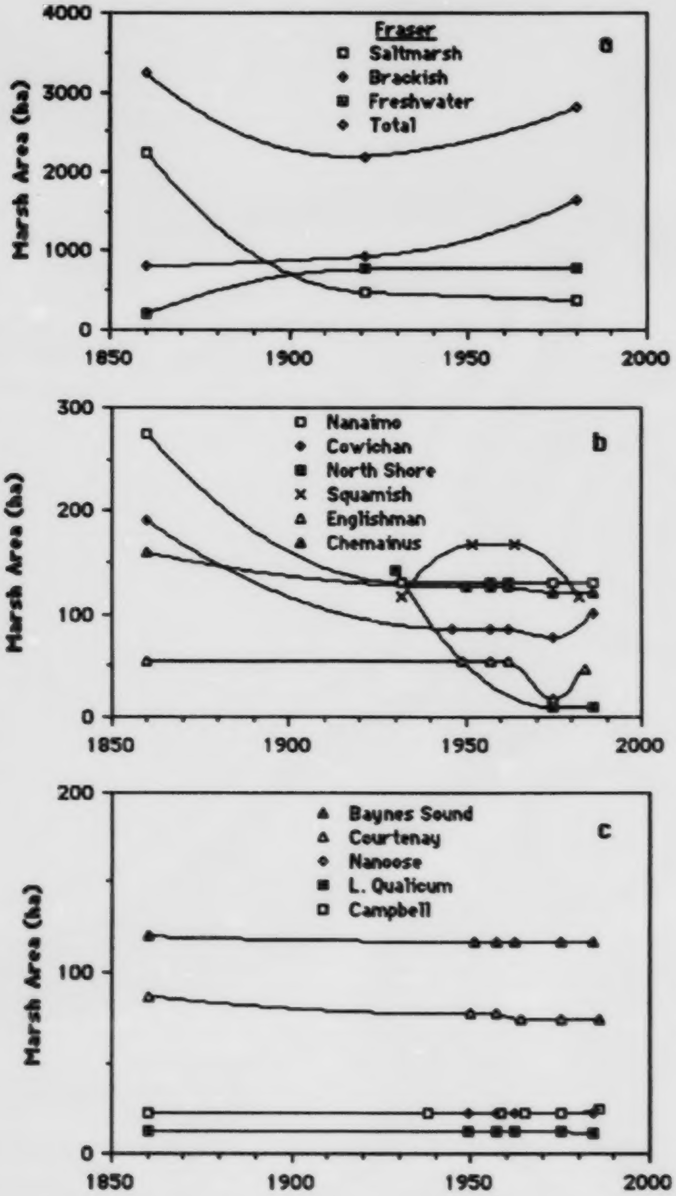
6. Community dynamics and habitat change

6.1. Alienation of estuarine habitat

The aboriginal peoples of coastal areas in British Columbia used intertidal marsh plants for food (especially *P. pacifica*, *G. maritima*, and *T. maritimum*) and as sources of material for basketry (*Scirpus* spp.) (Turner 1975, 1979). Prior to European settlement, however, the impact of local human populations on the aquatic plant resources of the Strait of Georgia was minimal. Intertidal habitats in the area have, however, been increasingly affected by man's activities since the first European settlers arrived in the 1860s (Campbell Prentice and Boyd 1988). At that time, some 4450 ha of intertidal marsh habitat existed in the Strait of Georgia. By the beginning of the present century, one-third of the intertidal marsh habitat in the strait had been diked for conversion to agriculture. The rate of habitat loss has been less dramatic in the last few decades and has been offset by gains as a result of marsh progradation. Nevertheless, considerable changes in the areal extent and spatial distribution of marsh habitat have occurred. On the basis of the data presented in Figure 8, we estimate that the total area of intertidal marsh in the Strait of Georgia at present is about 3650 ha, an increase of approximately 650 ha since the 1930s. Eighty percent of the total marsh area in the Strait of Georgia is located in the Fraser River estuary.

The pattern of change in individual marshes is shown in Figure 8. This graph indicates that the highest rates of habitat loss have taken place in the large and intermediate-sized estuarine systems; in smaller estuaries, the total marsh area has remained essentially static over this time period. The greatest losses occurred in the Fraser River estuary, where some 70% of former salt marsh and 30% of the freshwater marsh were lost (Romaine *et al.* 1976). These estimates are based on maps showing the distribution of vegetation types in the Fraser River delta at the time of the first land survey (North and Teversham 1976; North *et al.* 1979). Because the intertidal zone was not surveyed, seaward marsh margins are reconstructed by these authors from the present-day distribution of marsh habitat. Aerial photographs and maps from the 1920s and 1930s, however, indicate that the leading edge of the foreshore marshes of the Fraser River delta at that time was

Figure 8
Areal change in the extent of intertidal marshes in the Strait of Georgia from 1860 to the present: (*a*) Fraser River delta; (*b*) and (*c*) other areas discussed in the text (from Campbell Prentice and Boyd 1988; IH, unpubl. data)



several tens to hundreds of metres landward of its present location. We have assumed that the seaward edge of the marsh in 1930 is also its mid-19th-century position, although the foreshore marsh margin likely advanced in this time period (cf. Johannesen 1961). Figure 8*a* summarizes our reconstruction of the distribution of intertidal marsh in the Fraser River estuary in the mid-19th century and indicates no net loss of fresh and brackish marsh in the period 1860–1930.

The major losses in the present century have not resulted from continued agricultural conversion but from the industrial development and urbanization of this region. The "North Shore" deltas of Burrard Inlet (Capilano River, Seymour River, Lynn Creek) provide the most extreme example of loss of intertidal habitat: by 1975, 94% of the marsh area present in 1930 had been converted to industrial and associated land uses (Environment Canada 1975). In contrast, although Campbell Prentice and Boyd (1988) noted a loss of 23% of available "upland" deltaic habitat (meadow, pasture) during the last 40–50 yr in 14 estuaries on the east coast of Vancouver Island (primarily to residential development and log handling facilities), the loss of intertidal marsh and mudflat amounted to only 1.5% of the habitat area along this littoral.

The most notable loss of eelgrass and algal bed habitat in the Strait of Georgia in recent decades was associated with the construction of the Roberts Bank coalport on the Fraser River delta. Some 20% of a 350-ha eelgrass bed was lost as a result of dredging of the boat turning basin, but the reduced turbidity of tidal flows south of the coalport causeway has led to an increase in eelgrass shoot density and an expansion of the bed to higher levels in the intertidal zone (Beak Hinton Consultants Ltd. 1977; Luternauer *et al.* 1984).

6.2. Creation and rehabilitation of estuarine habitat

The losses in marsh habitat that have taken place in the Strait of Georgia in the last century are being mitigated in several ways. Some marsh areas are currently being restored by the deliberate breaching of dikes to return alienated land to intertidal habitat. Studies at the Englishman (Dawe and McIntosh 1987) and Cowichan (Campbell Prentice 1987) marshes and the Kokish marsh of northeastern Vancouver Island (Campbell and Bradfield 1988) have shown that dike breaching can have favourable results. Salt-intolerant upland species have been replaced by salt-tolerant sedges (*C. lyngbyei* and *Scirpus* spp.) and *Ruppia* within a few years of dike breaching. In addition, marsh creation projects involving vegetation transplants have been attempted in several estuaries, the most successful to date being the rehabilitation of a former log handling facility in the Campbell River estuary (Brownlee *et al.* 1984; Raymond *et al.* 1985).

6.3. Marsh progradation and community dynamics

The intertidal plant communities of the Strait of Georgia, as elsewhere, undergo change through time in area and community composition as a result of coastal erosion and sedimentation and changes in the hydrological regimes of local rivers. Areal expansion usually results from the colonization and stabilization of newly deposited sediments by rhizomes and seedlings. Rates of marsh progradation seem to be linked to the rate of sediment supply and the size of the contributing river. Marsh progradation on the Fraser River delta foreshore over the last five decades has been very extensive in the vicinity of distributary channels; over the entire foreshore it has averaged some 5.6 m·yr^{-1} (IH, unpubl. data). It is likely that the area of brackish and freshwater marsh at present is greater than it was in the mid-19th century. In the case of the Squamish River estuary, there was an advance in the foreshore marsh margin between 1932 and 1952 that added 51 ha of marsh to a preexisting total of 117 ha. An equivalent area has since been lost, however, as a result of port and industrial development and dredge spoil disposal (IH, unpubl. data). Progradation rates are much lower in the small, saline estuaries of Vancouver Island. In the Nanaimo River estuary, for instance, little change can be detected in the location of the foreshore marsh margin on aerial photographs extending from 1932 to the present.

Measurements of sediment accretion rates at 340 stakes on the marsh platforms of the Nanaimo, Fraser, and Squamish river deltas indicate substantial variation in annual vertical growth (IH, unpubl. data). The mean (± SE) annual accretion rate in the Nanaimo River delta marshes is 0.1 ± 0.4 mm; in the Fraser and Squamish river delta marshes, the equivalent values are 18 ± 2 and 8 ± 2 mm. If these short-term data are representative of long-term averages, the foreshore marshes of the Fraser and Squamish river deltas are capable of proceeding from a pioneer community at 2.5 m above chart datum to the upper marsh limit at 5.0 m above chart datum within about 400–500 yr. In contrast, the low sedimentation rate on the Nanaimo River delta means that the low-marsh areas that are currently forming will require several millennia to aggrade to a supratidal elevation. If the measured rates of vertical accretion on the Nanaimo River delta marshes are typical of the other small, salt-marsh-dominated estuaries in the Strait of Georgia, then the successional replacement rates on these deltas are likely an order of magnitude less than their brackish marsh counterparts. Although the extrapolation of these short-term data to long-term successional processes must be viewed with a great deal of caution, the reality of habitat change from natural processes holds profound implications for habitat management and waterfowl conservation.

7. Conclusions and recommendations for future research

Aquatic plants of intertidal and shallow subtidal habitats in the Strait of Georgia form the base of the food chain that supports the large migratory waterfowl populations. The main plants eaten by birds are sedges (*Carex*), bulrush (*Scirpus*), ditch-grass (*Ruppia*), eelgrass (*Zostera*), and some algae (mainly *Ulva* and *Enteromorpha*). In addition to the plant tissues, the birds may also be benefiting from a variety of other organisms (e.g., herring eggs) that occur on the plant surfaces.

The tidal marshes of the Strait of Georgia may be classified by salinity and geographic criteria into three general types:
(1) saline marshes, which occur mainly along the east coast of Vancouver Island and in Boundary Bay;
(2) brackish marshes, which occur at the mouths of the large rivers (e.g., Fraser, Campbell); and
(3) fjord-head marshes, found only along the mainland coast of the strait (e.g., Squamish, Indian).
These marsh types provide different kinds of habitat and food resources for birds; however, specific information on bird–habitat–plant interactions in most areas is unavailable. In the brackish marshes of the Fraser River delta foreshore, Snow Geese grubbing for *Scirpus* rhizomes in the low marsh in winter may affect microtopography and sedimentation patterns, thus indirectly affecting many other organisms dependent upon the marsh.

The major losses of intertidal habitat in the Strait of Georgia had occurred by the turn of the century as a result of agricultural diking. The main present-day threats are localized habitat losses from urban, agricultural, and recreational expansion, as well as habitat deterioration from pollution. New mudflats are continuously forming along the deltaic fronts of large rivers, such as the Fraser River, which eventually may become productive waterfowl habitat. Losses to agriculture have not been entirely negative from a waterfowl perspective, however, because diked fields provide alternative resting and feeding areas for dabbling ducks, geese, and swans during the winter months.

In planning future research on bird use of aquatic plant resources in the Strait of Georgia, we recommend that the following questions be addressed:

1. What are the seasonal, year-to-year, and longer-term use patterns of estuarine habitats by the regional avifauna, and how are these influenced by the availability and quality of food resources?
2. What are the interrelations between birds and other organisms (plants and animals) in the estuarine habitat, and how are these being affected by increasing environmental stress?
3. What kinds of impacts are habitat improvement projects, such as dike breaching, having on habitat quality, food plants, and bird use patterns?
4. From a broader perspective, what role do estuarine habitats in the Strait of Georgia play in the integrated system of coastal and wetland ecosystems along the Pacific Flyway?

Answers to these and related questions will lead to informed criteria for habitat conservation in the Strait of Georgia and could ensure the continued existence of healthy and diverse bird populations in this region.

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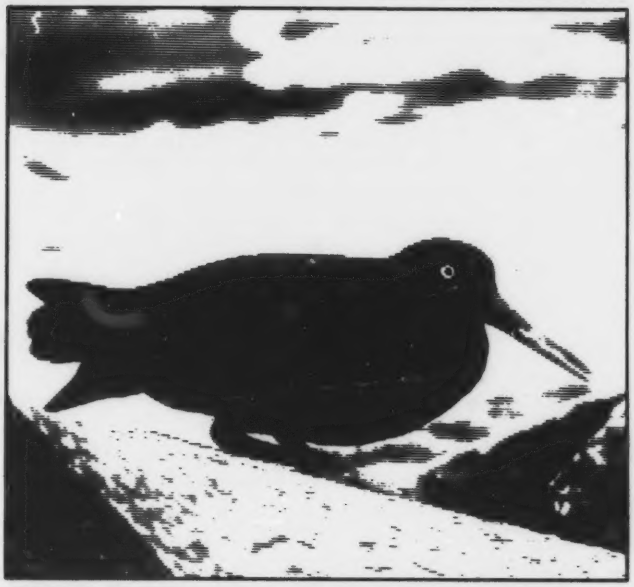
Part 2

Feeding ecology of marine and shoreline birds



Feeding ecology of marine birds in the Strait of Georgia

Kees Vermeer and Ronald C. Ydenberg

1. Abstract

The feeding ecology of marine birds in the Strait of Georgia is reviewed. The review indicates that we know something of the feeding ecology of 10 diving duck and three gull species, but little or nothing regarding that of 10 other common species—two species each of alcids, cormorants, grebes, gulls, and loons. Information gaps on the latter species must be addressed to understand the overall interactions of marine birds and their prey. An understanding of these interactions, the determination of the birds' prime feeding habitat, and an assessment of adverse effects of man's activities on birds are essential for preserving the highly diversified marine bird fauna in the Strait of Georgia.

2. Résumé

Les auteurs étudient l'écologie alimentaire des oiseaux marins dans le détroit de Georgia. L'étude indique que nous possédons certaines données sur l'écologie alimentaire de 10 espèces de canards plongeurs et de trois espèces de mouettes ou goélands, mais que, dans ce domaine, nous ne savons presque rien au sujet de 10 autres espèces communes — deux espèces d'alcidés, de cormorans, de grèbes, de mouettes ou goélands et de huards. Il faut suppléer le manque d'information sur ces dernières espèces afin de comprendre les interactions globales entre les oiseaux marins et leurs proies. Pour préserver la très grande diversité des oiseaux marins qui fréquentent le détroit de Georgia, il faut absolument comprendre ces interactions, connaître les endroits où les oiseaux s'alimentent de préférence et évaluer les effets nuisibles de l'activité humaine sur les oiseaux.

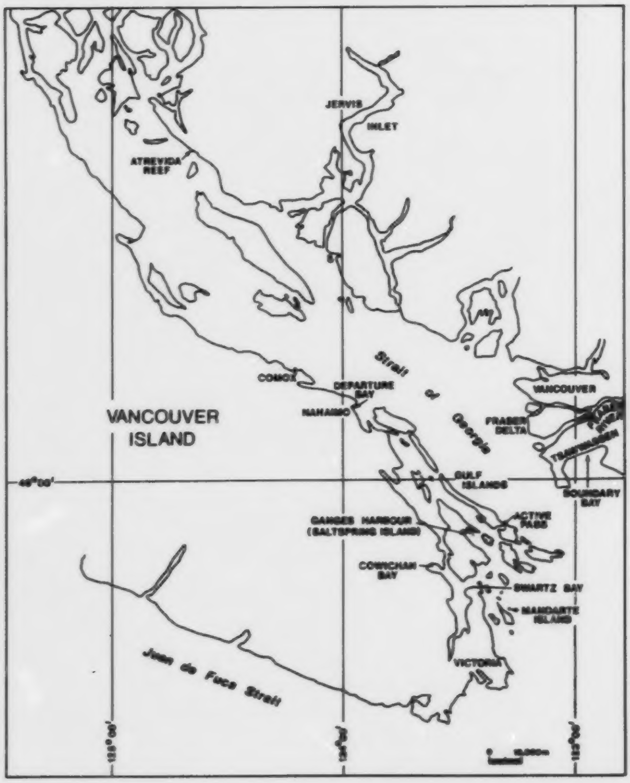
3. Introduction

Marine birds are defined here as birds that feed extensively in waters of the Strait of Georgia. Shorebirds have been omitted because, except for phalaropes, they are not found on the water, and dabbling ducks, geese, and swans feed only to a limited extent in the marine habitat.

Two groups of marine birds—nesting and nonnesting birds—forage in the Strait of Georgia. The chief nesting species are the Glaucous-winged Gull (*Larus glaucescens*), Pelagic Cormorant (*Phalacrocorax pelagicus*), Double-crested Cormorant (*P. auritus*), Pigeon Guillemot (*Cepphus columba*), and Marbled Murrelet (*Brachyramphus marmoratus*). A few Rhinoceros Auklets (*Cerorhinca monocerata*) and Tufted Puffins (*Fratercula cirrhata*) nest on Mandarte Island (Fig. 1). All the above species can also be present in the Strait of Georgia outside the nesting season. Many more marine bird species find shelter and forage in the strait during fall, winter, and spring than during summer; these include loons, grebes, cormorants, diving ducks, gulls, and auks.

Munro and Clemens (1931) made the first serious investigation of marine birds in relation to the spawning of herring in the Strait of Georgia. Other studies by Munro (1941, 1942) and Munro and Clemens (1937, 1939) also provided information on the diet of diving ducks in the strait. Drent (1965) examined the food habits of Pigeon Guillemots, and Robertson (1974) those of Pelagic and Double-crested cormorants during the nesting season on

Figure 1
The Strait of Georgia and localities mentioned in the text



Mandarte Island. Robertson (1973) briefly investigated the diet of Pacific Loons (*Gavia pacifica*), Brandt's Cormorants (*Phalacrocorax penicillatus*), Western Grebes (*Aechmophorus occidentalis*), Glaucous-winged Gulls, and Common Murres (*Uria aalge*) in the Gulf Islands during winter. Vermeer and colleagues examined the diet of diving ducks (Vermeer and Levings 1977; Vermeer 1981, 1982*a*, 1983*a*; Vermeer and Bourne 1984) and that of gulls (Vermeer 1982*b*; Vermeer *et al.* 1987).

The diet of nesting and wintering marine birds in the Strait of Georgia was reviewed briefly by Vermeer (1983*b*). The objectives of the present survey were to update that information, examining the birds' diet, food consumption, and their interaction with prey and predators. If there are insufficient data on the birds' food habits in the strait, we refer to studies dealing with the birds' diet elsewhere in the northeastern Pacific.

4. Diet during the nesting season

4.1. Glaucous-winged Gull

The Glaucous-winged Gull forages opportunistically, and its diet reflects prey abundance and accessibility. In the Strait of Georgia, adult Glaucous-winged Gulls eat mostly refuse and, to a lesser extent, bivalves—mostly blue mussels (*Mytilus edulis*)—and fishes—mainly Pacific herring (*Clupea harengus*)—during the early phases of nesting (Vermeer 1982*b*).

The Glaucous-winged Gull feeds frequently on human refuse that is readily available in refuse dumps near large cities bordering the strait. On the west coast of Vancouver Island, where there are no large cities and presumably less refuse, the gulls' diet consists of more intertidal invertebrates than refuse (Vermeer 1982*b*); here, gulls feed extensively on gooseneck barnacles (*Polliceps polymerus*) and California mussels (*Mytilus californianus*). Trapp (1979) found that on the Aleutian Islands in Alaska, some gull pellets contained mostly sea urchins, and others, mostly fish; in localities where storm-petrels and small auklets nested, the pellets contained mostly remains of those birds. Irons *et al.* (1986) observed that in the Aleutian intertidal zone, Glaucous-winged Gulls foraged mostly on barnacles (*Balanus glandula*) and blue mussels during neap low tides and on sea urchins (*Strongylocentrotus polyacanthus*), chitons (*Katherina tunicata*), and limpets (*Collisella pelta* and *Notoacmaea scutum*) during spring low tides. Barnacles and blue mussels were most abundant in the upper intertidal and sea urchins, chitons, and limpets in the lower intertidal.

Adult gulls in the Strait of Georgia feed their chicks mostly fishes—primarily juvenile herring, but also salmon, blennies, lampreys, and sculpins.

4.2. Double-crested and Pelagic cormorants

Little is known about the diet of adult Double-crested and Pelagic cormorants in the Strait of Georgia. However, the diet of chicks on Mandarte Island is known (Robertson 1974). The four most important food fishes of Double-crested Cormorant chicks by weight were penpoint gunnel (*Apodichthys flavidus*, 36%); shiner perch (*Cymatogaster aggregata*, 21%); crested gunnel (*Pholis laeta*, 16%); and snake prickleback (*Lumpenus sagitta*, 10%). Those of Pelagic Cormorant chicks were crescent gunnel (37%); Pacific sandlance (*Ammodytes hexapterus*, 19%); Pacific staghorn sculpin (*Leptocottus armatus*, 13%); and penpoint gunnel (11%). Robertson (1974) reported that most of those fishes are characteristic of the littoral benthic zone and suggested that the two cormorant species forage mostly in shallow water.

Ainley *et al.* (1981) analyzed pellets regurgitated by adult and subadult Double-crested and Pelagic cormorants on South Farallon Island, California. They observed little dietary overlap between the two species. The remains of athernids, *Porichthys* sp., embiotocids, engraulids, and sciaenids occurred mostly in pellets of Double-crested Cormorants; those of sculpins and rockfishes (*Sebaster* sp.) were present mostly in the pellets of Pelagic Cormorants. On the basis of those findings, Ainley *et al.* (1981) suggested that Double-crested Cormorants feed mostly upon schooling fishes in the water column over flat bottoms and Pelagic Cormorants mostly on nonschooling fishes off rocky reefs.

4.3. Pigeon Guillemot

Pigeon Guillemots feed near their colonies in inshore waters during nesting (Drent 1965). Little is known about the summer diet of the adult birds in the Strait of Georgia, but Drent (1965) found that parents delivered 10 categories of fish to their chicks on Mandarte Island. Benthic fish, such as blennies and sculpins, comprised at least 70% of these fishes. The chicks had difficulty swallowing any sea-poachers (which are armoured) and flat fish that were presented by the parents. Follett and Ainley (1976) found that epibenthic fish predominated in chick diets on south Farrallon Island, similar to what was found on Mandarte Island. Kuletz (1983) reported that sandlance and blennies made up the main diet of chicks at Naked Island, Alaska. Other prey consisted of herring, smelt, lingcod, cod, sculpins, flatfish, rockfish, squid, and shrimp. Krasnow and Sanger (1982) examined stomachs of adult birds from Kodiak Island, Alaska, during summer. They found that crabs (mostly *Cancer oregonensis*), capelin (*Mallotus villosus*), and Pacific sandfish (*Trichodon trichodon*) were the most important prey. From a comparison of the limited information on the diets of adults and chicks, it seems that adult Pigeon Guillemots eat fish and invertebrates, whereas parents feed their chicks chiefly fish.

5. Diet of birds outside the nesting season

5.1. Loons

Four species of loons visit the Strait of Georgia: the Pacific Loon, Common Loon (*Gavia immer*), Red-throated Loon (*G. stellata*), and Yellow-throated Loon (*G. adamsii*). Little is known about the diet of the last three species, but that of the Pacific Loon, which is by far the most common species of loon to visit the strait, was briefly examined by Robertson (1973). Of 16 Pacific Loon stomachs obtained from Active Pass, two were found to be empty, and 14 contained Pacific herring. Six undigested retrieved herring averaged 20.0 cm in length.

Reimchen and Douglas (1984) studied the feeding schedule and consumption of nesting Red-throated Loons in the Queen Charlotte Islands and reported that adults fed marine fishes to their young, almost exclusively. The diet consisted chiefly of Pacific herring, shiner perch, and smelt, but Pacific sandlance, gunnels, and snake prickleback were also present.

The diet of Common Loons in the northeastern Pacific is unknown, but Palmer (1962) reported that on the North American coast these loons feed upon amphipods, crabs, and shrimp.

5.2. Grebes

Five species of grebes—the Western Grebe, Red-necked Grebe (*Podiceps grisegena*), Horned Grebe (*P. auritus*), Eared Grebe (*P. nigricollis*), and Pied-billed Grebe (*Podilymbus podiceps*)—visit the Strait of Georgia. The Western Grebe, which comes from nesting colonies in the interior of North America, is the most common species of grebe to visit the strait (Vermeer *et al.* 1983). The sheltered waters of the strait and those of adjacent Puget Sound constitute the world's major wintering area for Western Grebes. The Horned Grebe is the second most common species; Red-necked and Eared grebes are also common; and the Pied-billed Grebe is the least common visitor.

Robertson (1973) collected 18 Western Grebes in the Gulf Islands in winter, but only two birds had food in their stomachs: one contained Pacific herring, and the other, shiner perch. Of 13 Western Grebes collected near a herring spawn area at Boundary Bay in March, 10 had food in their stomachs, and three did not (KV, unpubl. data). Of those with food, eight grebes had eaten herring, and six birds, herring eggs. Most stomachs with herring eggs also contained algae (*Enteromorpha* sp.), eelgrass (*Zostera marina*), and small snails, which may have been incidentally ingested with the herring eggs. Phillips and Carter (1957) collected 13 Western Grebes in Puget Sound in winter, of which six had empty stomachs and seven contained food. Of those with food, five contained Pacific herring, two shiner perch, two Pacific staghorn sculpin, one codfish, and one prickleback. The above observations indicate that herring is an important food of Western Grebes in the Strait of Georgia, as well as in Puget Sound.

Vermeer (1983*b*) collected 15 Horned Grebes off southern Saltspring Island in October 1978 and observed that they had eaten mostly shrimp and fish. Coonstripe shrimp (*Pandalus danae*), grass shrimp (*Hippolyte clarki*), and other shrimp species (*Heptacarpus* sp.) were found in nine stomachs. Digested fish were found in five stomachs.

Little is known about the diet of Red-necked and Eared grebes in the Strait of Georgia. Palmer (1962) reported that Red-necked Grebes ate herring, pilchards, sculpins, shrimp, and prawns, and Eared Grebes ate amphipods and mysids, on the North American coast.

5.3. Cormorants

Three species of cormorants—the Pelagic, Double-crested, and Brandt's cormorants—utilize the sheltered waters of the Strait of Georgia during fall, winter, and spring. Of those three species, the Brandt's Cormorant, which breeds in California and Oregon, is the most common visitor to the Gulf Islands (Vermeer 1977; Vermeer *et al.* 1983). Robertson (1973) collected eight adult Brandt's Cormorants from Active Pass and five adults from Porlier Pass in winter. All eight birds from Active Pass had eaten Pacific herring. Only one cormorant stomach from Porlier Pass contained herring, whereas the other four contained plainfin midshipman (*Porichthys notatus*), shiner perch, and striped seaperch (*Embiotoca lateralis*). The above observations suggest that Brandt's Cormorants feed chiefly on herring in Active Pass. Twelve undigested herring retrieved from Brandt's Cormorants averaged 19.3 cm in length.

Brandt's Cormorants also feed extensively upon Pacific herring that are spawning. Vermeer (1981) observed 9000 Brandt's Cormorants, but only 20 Double-crested and 500 Pelagic cormorants, feeding at a herring spawn area at Ganges Harbour in March 1978. Two Brandt's Cormorants, which were chased by boat, regurgitated adult herring. Munro and Clemens (1931) collected six Pelagic Cormorants near a herring spawn area in Nanaimo and found that the stomachs of two birds were empty, whereas those of the other four contained Pacific herring, blackeye goby (*Coryphopterus nicholsi*), rockfishes, blennies, and coonstripe shrimp, but no herring eggs.

The winter food of Brandt's Cormorants was examined at Monterey Bay by Baltz and Morejohn (1977) and Talent (1984). Baltz and Morejohn (1977) found that the food of six cormorants, collected offshore, consisted chiefly of midwater species such as juvenile rockfishes (*Sebastes* sp.), northern anchovy (*Engraulis mordax*), and market squid (*Loligo opalescens*). Talent (1984) collected 11 cormorants inshore and found that they had fed chiefly on bottom-dwelling species from a sand and a mud substrate. The principal prey was Pacific sanddab (*Citharichthys sordidus*); also eaten were English sole (*Parophrys vetulus*), plainfin midshipman, juvenile rockfishes, and Pacific saury (*Cololabis saira*).

5.4. Bay ducks

Diving ducks are divided in this paper into bay, sea, and fish-eating ducks. The most numerous wintering bay ducks in the Strait of Georgia are Bufflehead (*Bucephala albeola*), Barrow's Goldeneye (*B. islandica*), Common Goldeneye (*B. clangula*), and Greater Scaup (*Aythya marila*) (Vermeer 1982*a*; Vermeer *et al.* 1983). As their group name implies, those ducks predominantly occur in bays and other sheltered waters.

The food habits of the three *Bucephala* species in the Strait of Georgia in winter have been compared in detail by Vermeer (1982*a*), who summarized that on a weight basis, Barrow's Goldeneye ate mostly blue mussels, Common Goldeneye mostly crustaceans, and Bufflehead mostly crustaceans and snails. The above summary, however, does not reflect prey diversity. On a prey occurrence basis, it was found that all three *Bucephala* species ate blue mussels, whereas the Bufflehead also fed upon other bivalves, such as *Psephidia lordi* and *Macoma* sp. The diet of the *Bucephala* was particularly rich in snails: 16 species occurred in both Bufflehead and Common Goldeneye, and seven species in Barrow's Goldeneye. At least five species of crab were eaten by Common Goldeneye, three species by Bufflehead, and one species by Barrow's Goldeneye. Other crustacean prey were barnacles (*Balanus glandula*), shrimp (*Upogebia pugettensis* and *Crangon* sp.), gammarid amphipods, and isopods. All three species ate herring eggs, and the Bufflehead also ate fishes (*Hydrolagus colliei*, *Pholis* sp.). Algae and vascular plants were ingested by all three *Bucephala*.

The staple diet of Greater Scaup in the Strait of Georgia consists primarily of algae, vascular plants, snails, and bivalves (Munro 1941; Vermeer and Levings 1977). Munro (1941) examined 21 Greater Scaup stomachs from the Cowichan Bay - Comox region and found that snails occurred in 16, blue mussels in six, limpets in four, barnacle chutes in six, and sea lettuce (*Ulva* sp.) in seven stomachs. Vermeer and Levings (1977) examined 50 stomachs of scaup (42 obtained in winter and eight in summer) from the Fraser River delta foreshore and found that the diet, on a weight basis, consisted mainly of algae (60%), vascular plants (14%), and bivalves (10%). *Enteromorpha* sp. and *Ulva* sp. were the most important algae, *Batillaria attramentaria* (formerly *B. zonalis*) the most important snail, and blue mussel the most frequently identified bivalve. Vascular plant remains and seeds were not identified to species. Apart from their staples, Greater Scaup feed opportunistically on fish eggs. Munro (1941) and Vermeer (1981) observed large concentrations of Greater Scaup at herring spawn areas. Munro and Clemens (1931) collected three scaup from such an area and found that they had eaten herring eggs, as well as the eelgrass and algae to which the eggs were attached.

5.5. Sea ducks

Sea ducks, although commonly found in bays and other sheltered waters, occur more frequently along the open and less sheltered coastline of the Strait of Georgia than do bay ducks. Five common species of sea ducks in the strait are the Surf Scoter (*Melanitta perspicillata*), White-winged Scoter (*M. fusca*), Black Scoter (*M. nigra*), Oldsquaw (*Clangula hyemalis*), and Harlequin Duck (*Histrionicus histrionicus*).

The food habits of the three *Melanitta* species in the Strait of Georgia, like those of the three *Bucephala*, have been compared in detail by Vermeer and Bourne (1984), who reported that bivalves formed the main diet for all three species. On a wet-weight basis, Black and Surf scoters fed mostly on blue mussels, whereas White-winged Scoters ate chiefly a variety of clams, of which *Protothaca staminaea*, *Tapes philippinarium*, *Clinocardium nuttallii*, and *Saxidomus giganteus* were most important. White-winged Scoters ate more snails—particularly *Batillaria attramentaria*—at the Fraser River delta than did the other two scoter species. Black Scoters ate more errant polychaetes than did Surf and White-winged scoters, and Surf Scoters ingested fewer barnacles than did Black and White-winged scoters.

On a prey occurrence basis, the diet of White-winged Scoters was very diversified: at least 20 bivalve and 20 snail species were identified as prey for this species (Vermeer and Bourne 1984). In comparison, 12 bivalve and 14 snail species were observed to be food for Surf Scoters (Vermeer and Levings 1977; Vermeer 1981). The number of Black Scoters examined for food contents in the Strait of Georgia has been limited, and at present only five bivalve species (Vermeer and Bourne 1984) and 11 snail species (Munro and Clemens 1931; KV, pers. obs.) are known to be eaten by Black Scoters. Animal foods eaten—other than bivalves and snails—were crabs, shrimp, amphipods, isopods, echinoderms, and herring eggs by Surf Scoters (Vermeer 1981); crabs, shrimp, herring eggs, and the occasional fish by White-winged Scoters (Vermeer and Bourne 1984); and limpets, crabs, and herring eggs by Black Scoters (Munro and Clemens 1931; pers. obs.). In addition, all three scoter species ingested algae and vascular plants, whether incidentally or as "sought-for" food.

The Surf Scoter, which is the most common diving duck in the Strait of Georgia, also feeds opportunistically on herring spawn for about three weeks in March (Vermeer 1981). During that time, tens of thousands of Surf Scoters are observed at herring spawn areas in the strait, as well as near those along the west coast of Vancouver Island. The other two scoter species are also seen at herring spawn areas but in much smaller numbers than are the Surf Scoters.

The diet of Oldsquaws was investigated by Vermeer and Levings (1977) at the Fraser River delta during summer and winter. On a prey biomass basis, Oldsquaws ate mostly bivalves and snails in summer, and bivalves and crustaceans in winter. By far the most predominant bivalve eaten in summer was *Macoma* sp., whereas no bivalve predominated in the winter diet. Two other bivalve species (*Protothaca staminea* and *Clinocardium nuttallii*) were identified in summer, and five such species (*P. staminea*, *C. nuttallii*, *Kellia laperousii*, *Psephidia lordi*, *Glycymeris subobsoleta*) were identified in the Oldsquaw diet in winter. No snail species were identified in the summer diet, but at least seven species occurred in the winter diet. Crustaceans eaten by Oldsquaw in winter were, in order of importance, shrimp (*Crangon franciscorum*, *Pandalus* sp., *Tanais* sp., *Natantia* sp., and *Cumacea* sp.); amphipods (*Anisogammarus confervicolus*, *Atylus* sp., *Photis* sp., *Ampelisca* sp., *Corophium* sp.); isopods (*Idotea* sp.); and crabs (*Cancer productus* and *Telmessus cheiragonus*).

Oldsquaws also feed extensively on herring eggs in spring. Several thousand Oldsquaws were observed feeding at a herring spawn area at Ganges Harbour in March 1978 (Vermeer 1981). All stomachs of 16 Oldsquaws collected at a herring spawn area at Atrevida Reef in March 1977 contained herring eggs (KV, pers. obs.). On a wet-weight basis, herring eggs comprised 37%, grit and shell fragments 56%, algae 3.5%, snails (*Callistoma annulatum* and *Odostomia* sp.) 2%, and digested matter 1.5% of the food contents. The algae and small snails, as well as much of the grit, may have been incidentally ingested with eggs.

The diet of Harlequin Ducks in the Strait of Georgia has been investigated by Vermeer (1983*a*), who examined 55 esophagi and gizzards of ducks collected during March, October, and November. On a percent wet-weight basis, Harlequin Ducks ate snails and limpets (29.3%), fish and fish eggs (21.9%), crabs (15.9%), chitons (13.2%), algae (9.2%), bivalves (8.5%), amphipods (0.9%), shrimp (0.4%), echinoderms (0.4%), and barnacles (0.3%). The Harlequin Duck diet was very diversified in snails and limpets: 25 species were identified. Crabs eaten were *Cancer* sp., *Hemigrapsus oregonensis*, and *Pagurus* sp. Many of the hermit crabs (*Pagurus* sp.) were taken by the birds as occupants of *Littorina* shells. Chitons (*Tonicella lineata* and *Mopalia* sp.) were eaten more by Harlequin Ducks than by any other duck species in the strait. Blue mussels were the only bivalve prey encountered.

5.6. Fish-eating ducks

Whereas several bay and sea ducks eat the occasional fish, mergansers specialize in eating fish. Munro and Clemens (1937, 1939) found that Common Mergansers (*Mergus merganser*) and Red-breasted Mergansers (*M. serrator*) fed mostly on salmon eggs from November to January, and at other times on fishes (mostly sculpins [*Cottus asper*]), in freshwater streams of the Strait of Georgia. Munro and Clemens (1937) collected 12 Common Mergansers from the mouth of rivers and found that the birds had eaten mostly Pacific staghorn and tidepool sculpins (*Oligocottus maculosus*) and, to a lesser extent, Pacific herring, threespine stickleback (*Gasterosteus aculeatus*), rockfishes, shiner perch, bay pipefish (*Syngnatus grisoleneatus*), Pacific sandlance, and blennies. Crustaceans observed in all 12 stomachs consisted of isopods (*Exosphaeroma oregonensis*), shrimp (*Spirontocaris sitchensis*), and shore crabs (*Hemigrapsus nudus* and *H. oregonensis*). Munro and Clemens (1939) observed that the food of 14 sea-feeding Red-breasted Mergansers consisted mostly of Pacific staghorn sculpin and herring, as well as eulachons (*Thaleichthys pacificus*), blennies, salmon, sticklebacks, and rockfishes. Four Red-breasted Merganser stomachs also contained shrimp (*Pandalus* sp., *Spirontocaris* sp.) and crabs (*Lophopanopeus bellus*). Munro and Clemens (1931) collected two Common and three Red-breasted mergansers at a spawning site and found that both species had eaten herring but not their eggs.

A third merganser, the Hooded Merganser (*Lophodytes cucullatus*), is much less commonly seen in the Strait of Georgia, and little is known about its diet there. The stomach of one Hooded Merganser, collected near Saltspring Island in March 1977, contained mostly crescent gunnels but also crabs and snail fragments. Cottam and Uhler (1937) studied the stomach contents of 138 Hooded Mergansers from various fresh- and saltwater locations in the United States and found fishes of little commercial value (24.5%), game fishes (15.2%), fish fragments (4.2%), and crustaceans and aquatic insects (56.2%).

5.7. Gulls

A dozen gull species visit the Strait of Georgia, but only three species—the Glaucous-winged Gull, the Mew Gull (*L. canus*), and the Bonaparte's Gull (*L. philadelphia*)—are numerous there (Vermeer *et al.* 1983).

The diet of nesting Glaucous-winged Gulls has been previously discussed (Section 4.1). Of 16 adult Glaucous-winged Gulls collected in Boundary Bay in January 1974, one stomach was empty, seven contained refuse, five had shrimp (*Upogebia pugettensis*), four had crabs (*Telmessus cheiragonis*), three had blue mussels, four contained plant fragments, and one had fish remains (KV, unpubl. data). Munro and Clemens (1931) and Vermeer (1981) observed thousands of Glaucous-winged Gulls feeding on herring spawn in March. Munro and Clemens (1931) examined 25 esophagi and stomachs of Glaucous-winged Gulls collected at a herring spawn area near Departure Bay. They found herring eggs in only three stomachs, whereas 13 stomachs contained either eelgrass or algae to which the herring spawn had been observed to be attached. At least seven gull stomachs contained fish, herring being identified in three. One of the herring, present in the esophagus of a gull, was identified as a spent female. Munro and Clemens (1931) also collected 150 pellets regurgitated by Glaucous-winged Gulls at different herring spawn areas near Departure Bay in March 1928 and found that at least 33 pellets contained either herring egg capsules or ova. Most pellets, however, contained eelgrass and various species of algae to which the herring eggs had been attached. Nine pellets were chiefly composed of unidentified fish bones, which were thought to be those of spent herring. Glaucous-winged Gulls, however, are also known to make shallow plunge dives for herring. Robertson (1973) collected 12 adult Glaucous-winged Gulls in the Gulf Islands in winter and observed that only five stomachs contained food: three of those had herring, two had refuse, one contained decapod fragments, and one had insect fragments.

The diet of Mew and Bonaparte's gulls was examined at a tidal upwelling site in Active Pass, as well as in the vicinity of Active Pass, by Vermeer *et al.* (1987). In spring, at the upwelling locality, both species ate predominantly the euphausiid *Thysanoessa raschii*. In autumn, Bonaparte's Gulls fed mainly on the amphipods *Parathemisto pacifica* and *Calliopius laeviusculis*; only a few Mew Gulls were present. Year-round sampling of zooplankton at the upwelling site showed gull numbers to correlate with time of maximum upwelling and abundance of zooplankton prey in surface waters. Away from the upwelling site, both Bonaparte's and Mew gulls fed mostly on fishes and intertidal organisms, but also on zooplankton along tide lines. Most of the fishes eaten by Mew Gulls were Pacific herring, and those eaten by Bonaparte's Gulls were Pacific herring and Pacific sandlance. Besides intertidal invertebrates, Bonaparte's Gulls also hawk for insects (Vermeer 1983*b*).

Mew Gulls also feed opportunistically on herring spawn. Munro and Clemens (1931) and Vermeer (1981) reported that thousands of Mew Gulls congregated at herring spawn sites at Departure Bay and Ganges Harbour. Stomachs of six Mew Gulls collected at Departure Bay contained herring eggs and either algae or eelgrass. About 4000 Mew Gulls were observed feeding on eulachons near the mouth of the Fraser River on 2 May 1985 (R.W. Butler and KV, pers. obs.). Of six Mew Gulls collected there at that time, all contained eulachons ranging from 15 to 18 cm in length. Mew Gulls were observed to congregate near the spawning site of eulachons from mid-April until early May.

Two other species of gulls—the California Gull (*Larus californicus*) and Heermann's Gull (*L. heermanni*)—are common visitors to the Strait of Georgia in the late summer, but little is known about their diet.

5.8. Auks

Seven species of alcids utilize the waters of the Strait of Georgia; the Pigeon Guillemot, Marbled Murrelet, and Common Murre are the most common (Vermeer *et al.* 1983). Of these three, the winter diet is best known for the Common Murres. Robertson (1973) collected 19 Common Murres in the Gulf Islands in winter and found that three stomachs were empty, nine contained Pacific herring, six had shiner perch, and one contained decapod fragments. Of the herring eaten by the murres, about half were juvenile fishes. Munro and Clemens (1931) collected eight Common Murres in the vicinity of Nanaimo in March and found that all had eaten fish—Pacific herring could be identified in seven stomachs. The above observations indicate that Common Murres feed mostly on herring in the Strait of Georgia in winter.

The diet of Pigeon Guillemots in summer has been discussed previously (Section 4.3). Munro and Clemens (1931) collected four adult Pigeon Guillemots in February and March near Nanaimo and found that all had eaten small fishes (unidentified) and crabs (*Cancer* sp. and *Pagurus* sp.), three had eaten shrimp (*Crangon* sp.), and one had eaten herring eggs. Krasnow and Sanger (1982) examined 44 stomachs of adult Pigeon Guillemots from Kodiak Island and found that shrimp and fish were most important in winter (49 and 45%, respectively, by volume), crabs (mostly *Cancer oregonensis*) and fish in June (90%, mostly capelin [*Mallotus villosus*] and Pacific sandfish [*Trichodon trichodon*]), fish in July (79%, mostly capelin), and fish in August (90%, mostly capelin and gadoids). The results of those two investigations, as well as that of Drent (1965), suggest that Pigeon Guillemots eat more invertebrates in winter than in summer.

Munro and Clemens (1931) collected four Marbled Murrelets in March near Nanaimo and found that three contained fishes and three mysids. The diet of murrelets is better known in Barkley Sound (on the west coast of Vancouver Island), where Carter (1984) found that 43 breeding adults and 26 moulting birds in late summer and fall had fed primarily on Pacific herring and Pacific sandlance. Sealy (1975) observed that at Langara Island, in the Queen Charlotte Islands, the most important foods present in 75 adult and subadult murrelets were Pacific sandlance and *Thysanoessa spinifera* in April and May and Pacific sandlance in June and July.

One other alcid that also commonly utilizes the waters of the Strait of Georgia in winter is the Ancient Murrelet (*Synthliboramphus antiquus*). During some winters, about 2000 to 8000 of these murrelets feed in turbulent waters near Victoria (Vermeer 1983*b*), where they apparently eat mostly euphausiids (S.G. Sealy, pers. commun.).

6. Bird use in relation to food consumption

Consumption by the nesting seabird population in the Strait of Georgia can be estimated from daily food intake on the basis of body weight. Food intake is dependent on metabolic requirements of birds, as well as on caloric values and lipid content of prey. A small seabird will eat more food relative to its body size than will a larger bird, primarily because of the greater energy loss associated with its higher body surface/body weight (volume) ratio (e.g., Kendeigh 1970; Vermeer and Devito 1986). Nilsson and Nilsson (1976) considered the latter factor when estimating daily food consumption of wild piscivorous birds with the formula $\log F = -0.293 + 0.85 \log W$, where F = food consumption in grams per day and W = weight of bird in grams. With known breeding populations and body weight of nesting seabirds, the daily as well as seasonal (1 May – 31 August) consumption of those birds in the Strait of Georgia can be estimated. It is calculated that the populations of Glaucous-winged Gulls, Double-crested and Pelagic cormorants, and Pigeon Guillemots consume about 8 t daily and 1000 t of food over the nesting season (Table 1).

Marine bird populations in the Strait of Georgia at nonnesting times are not well known. Therefore, it is impossible to determine total food consumption for these populations. However, the data presented in Figure 2 provide some information on bird use of the strait during March–April and November. Using the same methods for calculating food consumption of nesting birds, it is estimated that the average daily food consumption for the 85.8 birds per kilometre of shoreline in March–April was 17 $\mathrm{kg \cdot km^{-1}}$, and for the 103.6 birds per kilometre in November, 20 $\mathrm{kg \cdot km^{-1}}$.

One can also estimate the consumption of a particular prey species at a specific locality. Below are examples of such an estimate for three prey items—euphausiids, herring and herring spawn, and blue mussels.

Bonaparte's Gulls chiefly eat euphausiids (mostly *Thysanoessa raschii*) in a tidal upwelling area in Active Pass from the beginning of April until mid-June (Vermeer *et al.* 1987). An estimated 4000 gulls per day feed at the upwelling site from mid-April until the second week of June (about 53 d). Body weight of Bonaparte's Gulls feeding in that area averaged 222 g (n = 30). Euphausiid consumption by gulls was estimated at 200 $\mathrm{kg \cdot d^{-1}}$, or 10.6 t over the 53-d period.

Table 1
Estimated food consumption by nesting seabirds in the Strait of Georgia during 1 May – 31 August

Species	No. of nesting birds	Mean body weight (g)
Glaucous-winged Gull	26 000	1160[a]
Double-crested Cormorant	4 000	(est.) 2000[b]
Pelagic Cormorant	4 800	(est.) 1800[b]
Pigeon Guillemot	1 000	450[c]
Total	35 800	

[a] Mean adult weight of 14 gulls from Boundary Bay, January 1974.
[b] From Palmer (1962).
[c] From Drent (1965).

Thousands of marine birds fed mostly upon herring spawn but also upon the herring themselves at Ganges Harbour, Saltspring Island, from 22 February until 31 March 1978 (Vermeer 1981). The average number of birds feeding upon herring and herring spawn was estimated at 5000, 10 000, 34 000, 55 000, and 20 000 during the last week of February and the first, second, third, and fourth weeks of March, respectively. At an estimated average body weight of 1200 g per bird, herring and herring spawn consumption by the birds at Ganges Harbour was estimated to be 7.4, 14.8, 50.2, 81.2, and 29.5 t per week, respectively.

Barrow's Goldeneyes and Surf Scoters chiefly feed upon blue mussels in mainland fjords of the Strait of Georgia (Vermeer 1981). The total consumption of the edible portion of mussels in one of these fjords—Jervis Inlet—from September 1986 through May 1987 was estimated to be 74 t for Barrow's Goldeneyes and 90 t for Surf Scoters (Table 2).

7. Feeding behaviour and interaction with prey

The most important aspect of the foraging behaviour of the 30 or so species discussed in this paper is that almost all obtain all their food by diving. Diving can be viewed as an optimal foraging problem (Ydenberg 1988) in which the bird adjusts its diving behaviour to maximize its rate of energy intake. To achieve this, the foraging must balance the costs and benefits of diving. We can think of a diver as a forager making excursions from a central place (the surface). Longer dives are better in the sense that the forager can find more or a larger prey, but costly in the sense that more energy is expended during the dive and more recovery time is spent on the surface between dives.

7.1. Bird movements in response to prey

In a series of papers, Wood (1985*a*, 1985*b*) and Wood and Hand (1985) described some of the feeding ecology of Common Mergansers along the east coast of Vancouver Island. Mergansers occur along shorelines throughout the Strait of Georgia during the winter, but in spring they move to freshwater streams where they prey on juvenile salmonids traveling to the strait. The studies by Wood and Hand demonstrate how mergansers are highly attuned to the availability of juvenile salmon, moving from the strait into freshwater streams—and between the streams—as the availability of fish changes (Fig. 3).

7.2. Prey movement in response to birds

Mergansers hunt visually and capture their prey in underwater pursuits. Donnelly (1985) and Donnelly and Dill (1984) showed that salmon fry are cryptic, and that their camouflage is highly specific not only to the particular stream in which they were born, but even to specific parts of that stream. This crypsis provides protection from visual predators such as mergansers. Further work on fry behaviour (Dill and Fraser 1984) demonstrated that fry also change their behaviour after exposure to predators. In particular, they reduce the distance they move to intercept drifting food particles. Mergansers are more likely to spot moving than stationary fry, and so the fry's response seems adaptive (Dill 1983). This antipredator response has an important consequence. By reducing their reactive dis-

Figure 2
Marine bird densities in the Strait of Georgia and adjacent inlets as observed during boat surveys, March–April and November 1977 (from Vermeer 1981)

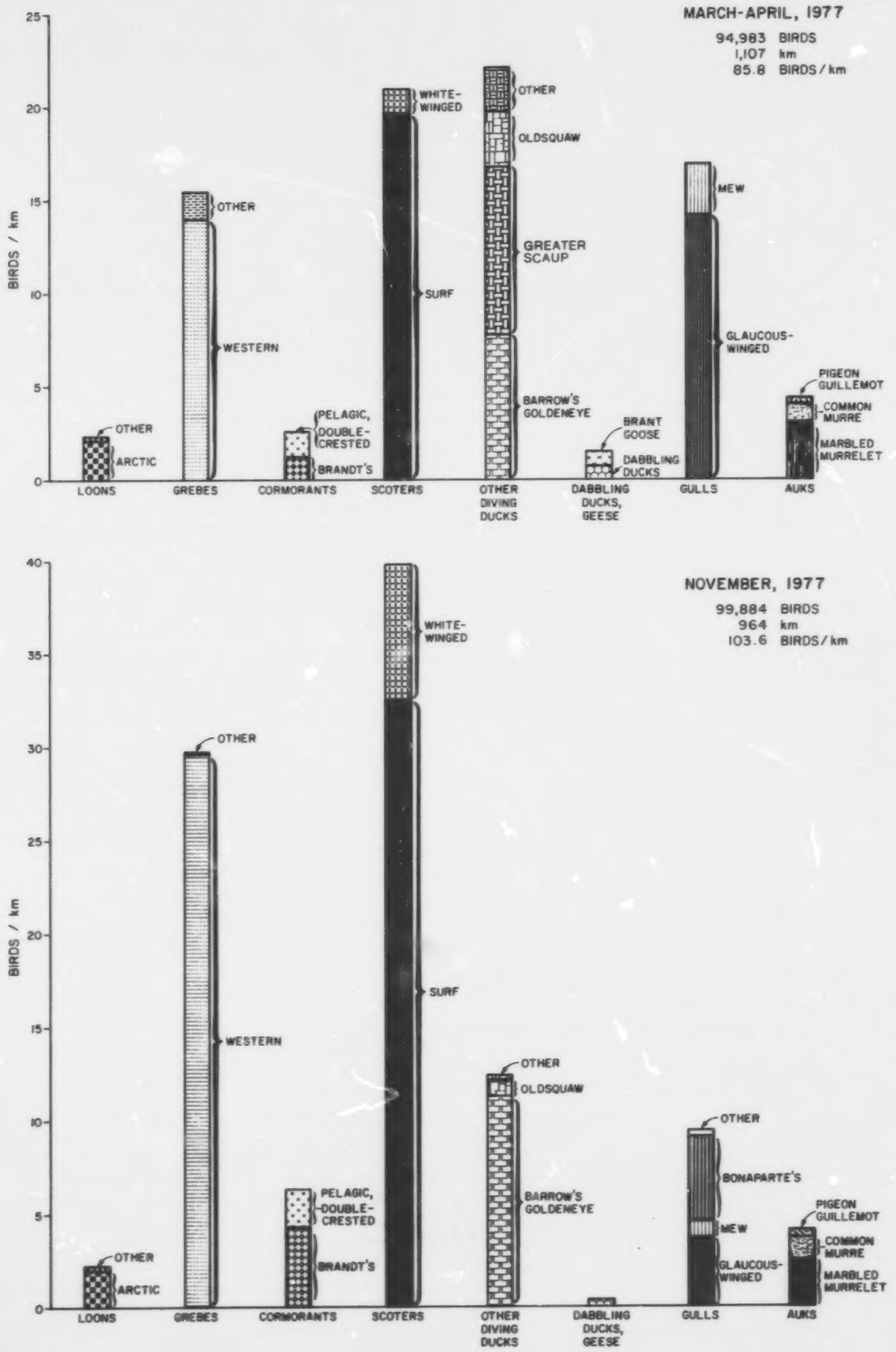


Table 2
Estimated consumption of blue mussels by Barrow's Goldeneye and Surf Scoters in Jervis Inlet, September 1986 – May 1987 (from Vermeer, Part 5, this publication)[a]

	No. of ducks observed		Calculated mussel consumption (kg)	
Monthly observations	**Barrow's Goldeneye**	**Surf Scoter**	**Barrow's Goldeneye**	**Surf Scoter**
September	5	320	27	1 882
October	145	2774	812	16 855
November	2134	2512	11 568	14 770
December	2642	2521	14 800	15 318
January	1715	2334	9 607	14 181
February	2185	1735	11 055	9 521
March	2656	1136	14 878	6 902
April	1548	539	8 392	3 169
May	482	1279	2 700	7 771
Total consumption			**73 839**	**90 369**

[a] No bird observations were made in February. Numbers in February were estimated from averaging numbers in January and March. Mussel consumption was calculated on average weight basis of 1000 g for Barrow's Goldeneyes and 1100 g for Surf Scoters (Vermeer 1981).

tance, fry gain less food and so grow more slowly, reducing their ocean survival. Juvenile salmon are therefore caught between opposing pressures—a large reactive distance produces fast growth at the expense of a high predation risk.

All prey that rely on camouflage to evade predators are faced with a similar dilemma, as they must move—thus breaking cover—in order to feed. Many fish preyed on by marine birds fall into this category, one good example being the sculpins (Cottidae). The same trade-off extends even to infaunal clams, another important prey item in the strait. Clams are excavated and eaten by a wide variety of predators, including a number of marine birds, most notably White-winged Scoters. Scoters dig pits in the substrate during dives (Glude 1964) and retrieve clams thus excavated to the surface, where they are swallowed whole and crushed in the muscular gizzard.

Although no research has been carried out in the Strait of Georgia, the work of Zwarts (1986) and Zwarts and Wannick (1984) in the Dutch Wadden Sea is illustrative of some potentially important principles. Their work showed that more deeply buried clams are safer from predators at the expense of being able to feed rapidly (Fig. 4). Clams reduce their burial depth after their siphons are cropped by fish and also if they are in poor condition, so that body reserves may be more rapidly recovered. Wadden Sea clams dig themselves deeper during the winter, apparently in response to an increased predation risk, but we know nothing about similar behaviour of clams in the Strait of Georgia.

The fundamental importance of the risk posed by predators to the ecology of all prey animals is just beginning to be appreciated by ecologists (Dill 1987). Vertical migration by zooplankton (Gliwicz 1986) and fish (Clark and Levy 1987) may be mentioned as recent examples demonstrating the importance of predation risk. The spines, sculpting, and architecture of bivalve and gastropod shells are another example (Palmer 1979; Boulding 1984). Because increasing the amount of carbonate shell necessary for spines or thicker shells slows the rate of body growth (Palmer 1981), this strategy also enhances safety at the expense of growth rate. The extent to which predation by marine birds has affected gastropods and bivalves in the Strait of Georgia is unknown.

7.3. Social behaviour

One of the most common sights in the Strait of Georgia during the winter is a flock of marine birds. One of the supposed functions of flocking is that flock members cooperate in hunting mobile prey, so that each individual flock member can feed faster. Wood and Hand (1985) measured the intake rate of Common Mergansers feeding in flocks in two different foraging situations in the Strait of Georgia and could find no evidence to support the cooperative hunting hypothesis. They suggested that flocks are simply the result of mergansers accumulating when and where the fishing is good. Flocks of diving birds often give the appearance of cooperation because they dive synchronously. Schenkeveld and Ydenberg (1985) showed that the level of diving synchrony in flocks of foraging Surf Scoters in the Strait of Georgia increased when Glaucous-winged Gulls were present. They surmised that the synchrony reduced the risk to each individual scoter of losing prey being retrieved to the surface to kleptoparasitic attack by gulls.

Not all diving birds feed in flocks. A recent discovery is that some Barrow's Goldeneyes maintain feeding territories during the winter (Savard 1986) and moreover occupy the same territories from year to year. Because many individual goldeneyes do not maintain territories but feed in mixed-species flocks, it would be interesting to investigate questions about territoriality in this species.

8. Recommendations for further studies

This brief review indicates that we know something of the feeding ecology of ducks and gulls in the Strait of Georgia but little or nothing regarding that of several species of alcids, cormorants, grebes, and loons. This deficit must be remedied before we can understand the overall interaction of marine birds and their prey. Some of the information gaps could be addressed by the following investigations:

(1) The winter diets of Common and Red-throated loons, Horned and Red-necked grebes, Double-crested and Pelagic cormorants, Marbled Murrelets, and Pigeon Guillemots and the late summer diets of California and Heermann's gulls are virtually unknown and should be investigated.

Figure 3
Movements of Common Mergansers in relation to the availability of juvenile salmonids in the Strait of Georgia and in streams draining into it (Map: RC = Rosewall Creek, BQ = Big Qualicum River, LQ = Little Qualicum River, ENG = Englishman River). (A) The proportion of the merganser population found on fresh water in the BQ, LQ, and ENG systems in relation to the juvenile salmonid migration. Mergansers move to fresh water as the migration intensifies. The points represent five census periods on each of the three streams. (B) The proportion of the total merganser population on the BQ (which accounts for 80% of the total migration). (C) Mergansers move to and from streams (in this case RC) in response to salmonid abundance. The solid line in the upper box shows the predictions of Wood's models (see text) (redrawn from Wood 1985a).

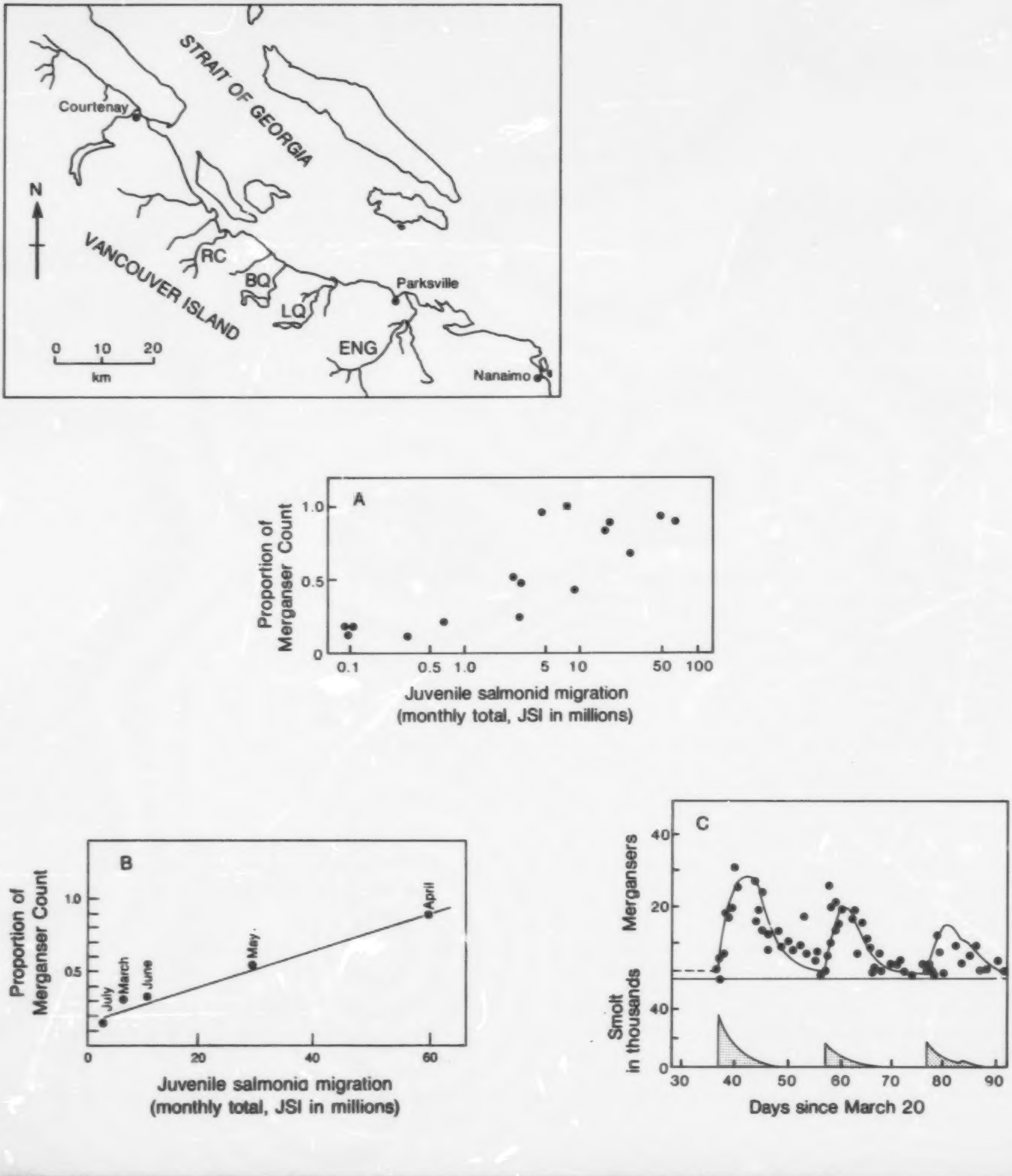
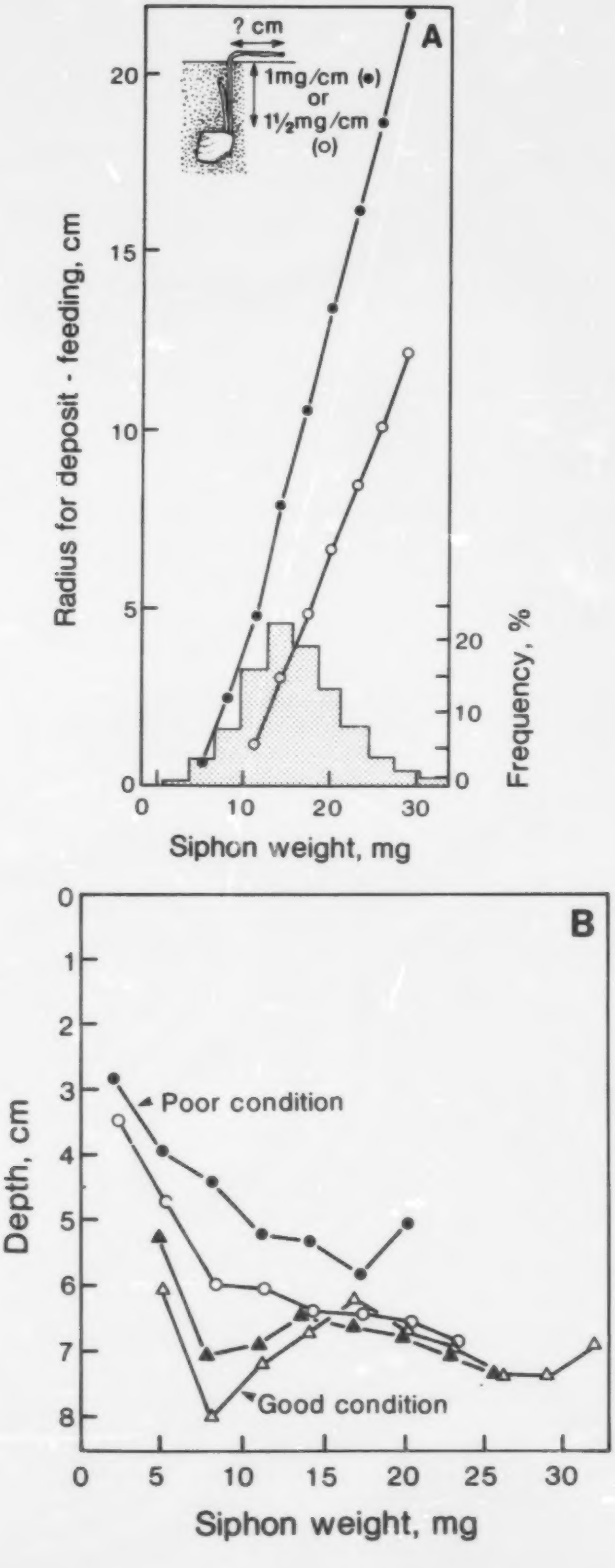


Figure 4
Burial depth of the infaunal clam *Scrobicularia plana*. Fish and benthic organisms crop the siphons of these clams, causing the animal to reduce its burial depth. More deeply buried clams are safer from predators. (A) The potential feeding radius as a function of siphon weight. (B) Clams in poor condition live at shallow depths, presumably to gain a feeding advantage, although at the cost of increased predation risk (redrawn from Zwarts 1986).



(2) The feeding habitat of alcids, cormorants, grebes, and loons in the Strait of Georgia should be investigated over the different seasons.
(3) The type and size of prey occurring in the diet of birds should be correlated with the distribution and abundance of prey found to determine prey availability and selection. The nutritional composition of major prey should be compared with that of the most abundant nonprey in the feeding substrate.
(4) Studies of diving and feeding behaviour and the energetics of most marine birds are required.
(5) The feeding ecology of whole marine bird communities and their interactions in specific feeding habitats should be determined.

More urgent than understanding the interaction between birds and their prey is the preservation of the marine birds themselves. Such birds, as well as their feeding habitat and food supply, are currently threatened by major man-made disturbances—destruction of feeding habitat, oil spillage, present fishing practices, and a rapidly expanding mariculture. Much habitat destruction has already occurred in the estuaries of the Strait of Georgia, and its effects on birds have been discussed by Butler *et al.* (this publication). The potential effects of oil spills on marine birds and their feeding habitat on the BC coast have been assessed by Vermeer and Vermeer (1975). The birds most likely to be directly affected by spills are the diving birds, whereas birds that feed in the intertidal zone may be hardest hit indirectly through destruction of their feeding habitat. Present fishing practices, particularly the harvesting of herring spawn, may detrimentally affect the birds, in that this wasteful fishing method (disregarding fishes that carry spawn) may deplete both herring stock and spawn.

The effects of an expanding mariculture in the Strait of Georgia on marine birds has not yet been assessed, but we can foresee several conflicts (Vermeer and Morgan, this publication). The birds' feeding habitat, already affected by the establishment and encroachment of harbours as well as by the effects of urban runoffs, industrial wastes from pulp and paper mills, chloralkali plants, and petroleum refineries, will be further eroded by the creation of fish farms. Farm operators may want to remove birds from the vicinity of farms as they prey upon fish stocks and spread diseases and parasites. Marine birds are known to disperse a variety of trematodes, which have a snail-fish-bird host sequence (Z. Kabata, pers. commun.).

To preserve marine birds, their habitat, and their food in the Strait of Georgia, we need to determine:
(1) prime feeding habitat of all marine birds—how much has been usurped by man, and how much is now left for bird use;
(2) marine bird - Pacific herring interactions, in relation to the utilization of Pacific herring and spawn by man and other predators;
(3) the consumption of prey alternatives (e.g., Pacific sandlance) to Pacific herring by marine birds;
(4) marine bird - euphausiid interactions in all tidally active areas; and
(5) effects of mariculture operations on bird populations, their feeding habitat, and prey.

9. Acknowledgements

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Feeding ecology of shoreline birds in the Strait of Georgia

Nicolaas A.M. Verbeek and Robert W. Butler

1. Abstract

The food habits of shoreline birds in the Strait of Georgia are still poorly understood, although published data exist for 11 species. The most detailed study is on the Great Blue Heron (*Ardea herodias*) during summer. This bird feeds mostly on small fish and shrimps caught in eelgrass (*Zostera*) beds. Waterfowl studies emphasize the importance of estuarine marsh plants in the strait and suggest that invertebrates might also be important. Bald Eagles (*Haliaeetus leucocephalus*) are primarily scavengers but also catch live fish and birds. Little is known about the diet of over 30 species of shorebirds that use the strait, except for Dunlins (*Calidris alpina*), which apparently eat mostly gastropods, bivalves, crustaceans, and insects during winter. When feeding on the shore, the Northwestern Crow (*Corvus caurinus*) eats mostly clams, crabs, and small fish. Herons, swans, geese, ducks, and shorebirds feed diurnally and nocturnally.

2. Résumé

Les habitudes alimentaires des oiseaux de rivage du détroit de Georgia sont encore peu connues même si des données à ce sujet ont été publiées dans le cas de 11 espèces. L'étude la plus complète a été faite au sujet de l'alimentation du Grand héron (*Ardea herodias*) pendant l'été. Cet oiseau se nourrit principalement de petits poissons et de crevettes prises dans les herbiers de zostères (*Zostera*). Les études sur les oiseaux aquatiques soulignent l'importance des plantes des marais estuariens dans le détroit et indiquent que les invertébrés pourraient également être importants. L'Aigle à tête blanche (*Haliaeetus leucocephalus*) est surtout nécrophage, mais il se nourrit aussi de poissons et d'oiseaux vivants. On connaît peu de choses au sujet de l'alimentation de plus de 30 espèces d'oiseaux de rivage qui fréquentent le détroit, sauf en ce qui concerne le Bécasseau variable (*Calidris alpina*) qui, apparemment, se nourrit surtout de gastropodes, de bivalves, de crustacés et d'insectes pendant l'hiver. Lorsqu'elle cherche sa nourriture sur le rivage, la Corneille du Nord-Ouest (*Corvus caurinus*) mange surtout des coquillages, des crabes et des petits poissons. Les hérons, les cygnes, les oies, les canards et les oiseaux de rivage se nourrissent le jour et la nuit.

3. Introduction

This paper deals with the food and the feeding behaviour of birds that regularly feed in tidal marshes, mudflats, seashores, and nearshore shallow waters in the Strait of Georgia. Intertidal marshes and mudflats are found primarily at the mouths of rivers and along the shores of shallow coastal bays. Of these, the marshes and mudflats at the mouth of the Fraser River and in adjacent Boundary Bay are by far the largest and provide an important food source for migrating and wintering birds (Butler and Campbell 1987). This fact, however, does not negate the importance of over 200 smaller estuaries scattered along the coast of the Strait of Georgia. The importance of the intertidal marshes and mudflats as loafing and feeding areas for birds has been stressed by many authors, including Brooks (1923), Smith and Blood (1972), Benson (1964), Burgess (1971), and Vermeer and Levings (1977). However, detailed studies of the diets of most shoreline birds in the Strait of Georgia are lacking.

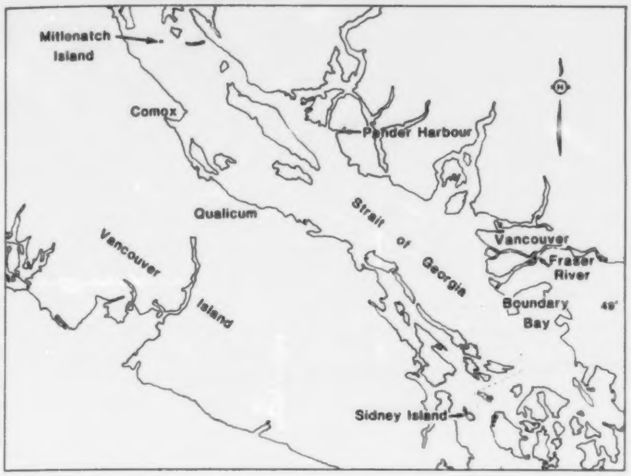
The feeding ecology of the following species in the Strait of Georgia has been investigated: Great Blue Heron (*Ardea herodias*), Trumpeter Swan (*Cygnus buccinator*), Snow Goose (*Chen caerulescens*), Green-winged Teal (*Anas crecca*), Mallard (*A. platyrhynchos*), Northern Pintail (*A. acuta*), American Wigeon (*A. americana*), Bald Eagle (*Haliaeetus leucocephalus*), American Black Oystercatcher (*Haematopus bachmani*), Dunlin (*Calidris alpina*), and Northwestern Crow (*Corvus caurinus*). The results are reviewed in this paper. In addition, new information is provided on the feeding ecology of the Northwestern Crow on Mitlenatch Island in the northern end of the Strait of Georgia. We include eagles and crows among the aquatic shoreline birds, because much of their food is obtained along the shore. Place names used in the text are shown in Figure 1.

4. Great Blue Heron

The feeding ecology of the Great Blue Heron in the Strait of Georgia has been studied near Vancouver (Paine 1972; Krebs 1974), on the Sunshine Coast (Kelsall and Simpson 1980; Forbes and Simpson 1982; Simpson 1984), and on Sidney Island (RWB, unpubl. data).

Herons from a colony located in the Endowment Lands of the University of British Columbia in Vancouver fed along sand- and mudflats of the Fraser River delta that were exposed at low tide, as well as in the "reed-covered tidal areas" of Sea Island, Westham Island, and Lulu Island (Paine 1972). Flocks ranged from one to 42 birds, usually four to 10, and remained mostly in water 15–30 cm deep by moving as the tidal levels changed (Paine 1972).

Figure 1
Place names mentioned in the text



Krebs (1974) found that the catch rate of herons feeding in the Fraser River delta increased with flock size and suggested that arriving herons used flock size to determine the profitability of feeding in specific areas. In contrast, Forbes and Simpson (1982) found that herons at Pender Harbour tended to feed alone, perhaps because the food supply there was more abundant and more evenly distributed than in the Fraser River delta. Herons caught significantly more prey during ebb than during flood tides, and more in deep water (up to the feathers on the thighs) than in shallow water (Simpson 1984; Table 1). The rate of prey capture at Farm Bay in Pender Harbour was highest at tide levels between 2.1 and 2.6 m above datum (Simpson 1984). Below 2.1 m, the bay was essentially dry, and prey intake stabilized around 7–9 g per 10-min feeding bout. Above 2.6 m, the water in most of the bay was too deep, so the birds were confined to the shores. The eelgrass (*Zostera marina*) zone and the tidal marshes along the shore provided the highest foraging success rate (Simpson 1984). Herons elsewhere around the Strait of Georgia—such as the colonies on Sidney Island, Shoal Island, Gabriola Island, Crescent Beach, Point Roberts, and at Pender Harbour and Sechelt—nest near, and feed in, eelgrass beds.

Kelsall and Simpson (1980) found that, from April to early July, the mean number per prey species, number of species, and the weight of individual fish caught per 10-min observation period increased linearly with prey abundance. After early July, prey abundance and catch rates declined.

The following data on food habits were obtained in Farm Bay in Pender Harbour (Forbes and Simpson 1982). At tides above 2.6 m—when the birds were confined to the shores of the bay—they caught mostly Pacific staghorn sculpin (*Leptocottus armatus*) and tidepool sculpin (*Oligocottus maculosus*). At tidal heights of 2.6–2.1 m, the mudflats became available, and the most common prey species of the herons were the arrow goby (*Clevelandia ios*), marine worms (*Nereis limnicola* and *N. brandti*), blue mud shrimp (*Upogebia pugetensis*), and red ghost shrimp (*Callianassa californiensis*). The eelgrass zone, the last to become available during ebb tides, was inhabited by all the above organisms. In addition, the following prey species were taken there: three-spined stickleback (*Gasterosteus aculeatus*), saddleback gunnel (*Pholis ornata*), starry flounder (*Platichthys stellatus*), shiner perch (*Cymatogaster aggregata*), chum salmon fry (*Oncorhynchus keta*), and bay pipefish (*Syngnathus griseolineatus*). Herons at Sechelt also fed on beaches dominated by eelgrass, and mostly on the same species as at Pender Harbour (Forbes and Simpson 1982), as well as on plainfin midshipman (*Porichthys notatus*).

On Sidney Island, 347 prey items taken by 98 herons in eelgrass beds included gunnels (*P. ornata* and *P. laeta*, 48.4%), staghorn sculpin (24.2%), shiner perch (14.1%), three-spined stickleback (9.2%), bay pipefish (2.3%), and chum salmon (1.7%) (RWB, unpubl. data). Table 2 lists known prey species of the Great Blue Heron in the Strait of Georgia.

5. Swans, geese and ducks

5.1. Food habits

At Comox Harbour estuary, McKelvey (1981) determined that rhizomes of three-square bulrush (*Scirpus americanus*) were the predominant food of wintering Trumpeter Swans. The microscopic analysis of 65 swan droppings collected on the estuary showed that the birds fed on eelgrass leaves (frequency of occurrence 33.8%), the rhizomes of bulrushes (30.8%), grass (18.5%), sedges (13.8%), and unidentified material (3.1%). Animal matter appeared to contribute very little to the diet of the swans. Butler (1973) and McKelvey (1981) reported occasional feeding on salmon carcasses.

Large numbers of Snow Geese winter along the shores of the Fraser River delta. Although they graze in pastures and fields, most of their food is obtained by grubbing for plant rhizomes in the tidal marshes. Burton (1977)

Table 1
Factors affecting the weight of prey caught by Great Blue Herons in tidal feeding areas at Pender Harbour (from Simpson 1984)

Parameter	Mean weight (g) caught/ 10-min trial	SD	*n*	*F*	Level of significance
Tide direction					
Ebb	13.86	10.5	556	9.4	0.002
Flood	11.48	12.3	336		
Water depth					
Dry	5.19	3.4	9		
Lower tarsus[a]	11.95	11.1	161		
Below ankle[b]	12.60	9.9	378		
Above ankle[b]	12.31	9.6	211		
Feather	17.55	16.2	148	7.7	<0.0001

[a] Referred to as "ankle" by Simpson (1984).
[b] Referred to as "knee" by Simpson (1984).

Table 2
Prey species of the Great Blue Heron in the Strait of Georgia (from RWB, unpubl. data; Krebs 1974; Redfield *et al.* 1977; Forbes and Simpson 1982)

Common name	Scientific name
Tubesnout	*Aulorhynchus flavidus*
Threespine stickleback	*Gasterosteus aculeatus*
Penpoint gunnel	*Apodichtys flavidus*
Crescent gunnel	*Pholis laeta*
Saddleback gunnel	*P. ornata*
Padded sculpin	*Artedius fenestralis*
Tidepool sculpin	*Oligocottus manulosus*
Buffalo sculpin	*Enophrys bison*
Pacific staghorn sculpin	*Leptocottus armatus*
Plainfin midshipman	*Porichthys notatus*
Bay pipefish	*Syngnathus griseolineatus*
Arrow goby	*Clevelandia ios*
Pacific sanddab	*Citharichthys sordidus*
Starry flounder	*Platichthys stellatus*
Shiner perch	*Cymatogaster aggregata*
Pacific sandfish	*Trichodon trichodon*
Pacific herring	*Clupea harengus*
Chum salmon	*Oncorhynchus keta*
Red ghost shrimp	*Callianassa californiensis*
Blue mud shrimp	*Upogebia pugettensis*
Grass shrimp	*Crangon* sp.
Isopod sp.	*Idothea resecata*
Nereid worm	*Nereis limnicola* and *N. brandti*
Townsend's vole	*Microtus townsendii*
Creeping vole	*M. oregoni*

Table 3
The aggregate percentage and frequency of occurrence of food found in the esophagus, proventriculus, and gizzards of 90 Snow Geese shot in the Fraser River delta (modified from Burton 1977)

Food item	Aggregate percentage (*n* = 75 birds)	Frequency of occurrence (*n* = 88 birds)
Bulrush rhizomes[a] (*Scirpus americanus* and *S. pallidus*)	74.7	76.1
Three-square bulrush shoots (*Scirpus americanus*)	9.3	17.0
Lyngby's sedge rhizomes (*Carex lyngbyei*)	6.7	8.0
Pale bulrush tubers (*Scirpus pallidus*)	2.7	2.3
Lyngby's sedge shoots (*Carex lyngbyei*)	0.0	1.1
Pale bulrush shoots (*Scirpus pallidus*)	0.0	1.1
Three-square bulrush seeds (*Scirpus americanus*)	0.0	1.1
Unidentified	6.7	5.7

[a] Rhizomes of three-square bulrush and pale bulrush could not be quantified separately.

analyzed the contents of the esophagus, proventriculus, and gizzard of 90 Snow Geese shot by hunters during two consecutive winters. The main food of the geese was the rhizomes of three-square bulrush and pale bulrush (*Scirpus pallidus*), which occurred together in 76% of the birds (Table 3).

The crop and gizzard contents of Mallard, Northern Pintail, Green-winged Teal, and American Wigeon shot by hunters along the foreshore of the Fraser River delta were analyzed by Burgess (1971). Although the ducks contained food derived from the intertidal marshes and from agricultural fields, "there was no difficulty in determining from which feeding area a food item had been taken" (Burgess 1971). In all four species of duck, softstem bulrush (*Scirpus validus*), three-square bulrush, and Lyngby's sedge (*Carex lyngbyei*) were important food plants (Table 4).

Burgess (1971) observed that Mallard, Northern Pintail, and Green-winged Teal ate mostly seeds in estuaries, whereas American Wigeon ate mostly vegetation on agricultural fields. However, the results might be biased against soft-bodied, easily digested plants and invertebrates, which would not remain long in the digestive tracts. Burgess (1971) also stated that his sample sizes may have been too small and that many birds contained too little food to draw definite conclusions. Indeed, Eamer's (1985) study in the Qualicum Beach region on Vancouver Island showed that the esophagi of 23 American Wigeon and 16 Mallards that had fed in tidal marshes and sloughs contained a greater variety of food than reported by Burgess (1971) for birds on the Fraser River foreshore. The esophagi she analyzed contained seeds, stems, roots, and algae. In addition, Mallards took gastropods (*Barlecia acuta*), bivalves (*Mya arenaria*, *Macoma* sp.), polychaetes, arachnids, isopods, amphipods, and eggs, larvae, and pupae of insects. Similarly, Vermeer and Levings (1977) found algae (*Ulva*, *Enteromorpha*, and *Lola lubrica*) in the esophagi and stomachs of five Gadwall (*Anas strepera*) and 10 American Wigeon collected off Iona Island in the Fraser River delta.

Several other species of waterfowl feed in the coastal marshes and the shallow water along the shore (Leach

Table 4
The composition of the food consumed by four species of duck in the Fraser River foreshore marshes (modified from Burgess 1971)

Food item	Importance value[a]			
	Mallard (189)[b]	Northern Pintail (98)	Green-winged Teal (75)	American Wigeon (115)
Lyngby's sedge (*Carex lyngbyei*)	1936	830	306	42
Softstem bulrush (*Scirpus validus*)	821	815	384	5
Three-square bulrush (*Scirpus americanus*)	234	218	474	14
American waterplantain (*Alisma trivialis*)	93			
Creeping spike-rush (*Eleocharis macrostachya*)[c]	32	16	118	1
Pale bulrush (*Scirpus pallidus*)	0	24	0	0
Seaside arrow-grass (*Triglochin maritimum*)	0	7	0	0

[a] Importance value = % volume × % frequency.
[b] Sample sizes are in parentheses.
[c] *E. macrostachya* = *E. palustris* (Hitchcock and Cronquist 1976).

1972; Butler and Campbell 1987). Many of these, such as Brant (*Branta bernicla*) and Canada Goose (*B. canadensis*), occur in large numbers, whereas others, such as Northern Shoveler (*Anas clypeata*), are rarer. Little information on their feeding habits in the Strait of Georgia is available.

5.2. Feeding behaviour

Trumpeter Swans at Comox Harbour feed on emergent vegetation by pulling up rhizomes. At low tide, the swans dig craters with their bills while standing or sitting, but at high tide they use their feet to loosen the soil and then grub for rhizomes with their bills (McKelvey 1981). The Trumpeter Swans at Comox Harbour spend a relatively small proportion of their time feeding while on the estuary. McKelvey (1981) determined that they fed for 38% of the daylight hours and 25% of the night. The rest of the time was devoted to other activities, such as swimming, preening, and sleeping. Similarly, Eamer (1985) reported that the dabbling ducks she studied on the east coast of Vancouver Island fed at night during full moon.

Burgess (1971) found that about half the ducks he studied were associated with tidal marshes. Of the four species in his study, American Wigeon represented 42% of the birds on the marsh, Green-winged Teal 29%, Mallard 16%, and Northern Pintail 13%. Eamer (1985), who studied Mallard and American Wigeon along the east coast of Vancouver Island, found that the number of ducks feeding on coastal intertidal habitats varied with the presence or absence of nearby flooded agricultural fields. Flooded fields attracted ducks, so that the number on the coast declined. A similar correlation between the degree of flooding of fields and its influence on the number of birds in coastal habitats was demonstrated for the Fraser River foreshore (Hirst and Easthope 1981). In contrast, freezing weather (Eamer 1985) and snow (McKelvey 1981) resulted in an influx of birds to the coast.

Burton and Hudson (1978) found that, on average, Snow Geese fed 7.2 h per 24-h day and rested for 12.4 h. Resting and feeding were closely correlated with location and tidal level. Feeding occurred mostly when the tidal levels were between 2.1 and 3.4 m, whereas resting occurred mostly when the levels were below 2.1 m or above 4.4 m. At tidal levels of 2.1–3.4 m, the rhizomes are covered by an average of about 15 cm of water. At a water depth over 20 cm, it becomes impossible for geese to properly brace themselves to extract the rhizomes. On the other hand, if the rhizomes are not covered by enough water, it becomes difficult to rid them of the adhering silt and fine roots. As food availability is determined by tidal level, feeding can occur both by day and by night, whenever tide level permits it. Because most food is located largely by the sense of touch, feeding can occur during night or day.

6. **Bald Eagle**

The Bald Eagle feeds on carrion, catches live prey, including birds, and steals food from other species. Retfalvi (1965, 1970) studied the food habits of this species on San Juan Island, a few kilometres south of the Strait of Georgia. Food habits were determined both by direct observation at two nests and by searching for accumulated food remains below the nest. The only mammal remains found below the nests were feral domestic rabbits (*Oryctolagus cuniculus*), which were picked up as carrion on the island's roads. In spite of the abundance of sheep on the island, the eagles were not seen to kill adults or lambs, but they did feed on carcasses and afterbirths. No sheep remains were found below the nests. Similarly, a stranded harbour seal (*Phoca vitulina*) was fed on *in situ* on the beach. The most important fish remains found below nests belonged to rockfish (*Sebastodes* = *Sebastes*) and lingcod (*Ophiodon elongatus*). Additionally, the eagles took cabezon (*Scorpaenichthys marmoratus*), arrowtooth flounder (*Atheresthes stomias*), and red Irish lord (*Hemilepidotus hemilepidotus*). A Bufflehead (*Bucephala albeola*) was brought to the nest, whereas the remains of gulls (*Larus*), Surf Scoters (*Melanitta perspicillata*), and Common Murres (*Uria aalge*), as well as those of some unidentified birds, were found below the nest. Other species included a crab (*Cancer* sp.) and a frog or toad. Vermeer, Morgan, Butler, and Smith (this publication) examined food remains below nests in the Gulf Islands in 1987 and found the major prey species to be Glaucous-winged Gulls (*Larus glaucescens*), rockfish, and lingcod.

7. **Shorebirds**

Thirty-four species of sandpipers regularly pass through the Strait of Georgia on their annual north- and southward migrations (Munro and Cowan 1947). Some of those species, such as Dunlin, Black-bellied Plover (*Pluvialis squatarola*), and Sanderling (*Calidris alba*), remain during the winter, whereas others, such as American Black Oystercatcher and Killdeer (*Charadrius vociferus*), are year-round residents. We know little about what they eat while in the Strait of Georgia. The only species that has been studied in detail in the Strait of Georgia is the Dunlin. McEwan and Farr (1985) and McEwan and Gordon (1985) studied the distribution of benthic invertebrates and their abundance in Boundary Bay and Roberts Bank to document the spatial and temporal changes in the distribution of food organisms potentially available to Dunlin. The highest mean densities of major invertebrate taxa occurred adjacent to salt marshes in the eastern end of Boundary Bay. McEwan and Fry (1985) analyzed the contents of the esophagus and stomach of 171 Dunlin collected on Mud Bay from November 1979 to April 1980. Their list of food items included polychaete and oligochaete worms; gastropods (*Acmaea*, *Bittium*, *Lacuna*, *Nassarius*, and *Olivella*); bivalves (*Macoma*, *Mytilus edulis*, and *Protothaca*); crustaceans (*Corophium*, *Hemigrapsus oregonensis*, and *Tanais stanfordi*); and remains of an unidentified insect. Plant material, particularly seeds of *Carex* and *Rumex*, was reported in most stomachs.

American Black Oystercatchers feed along open, rocky coasts from the highest tide line, above which the rock is mostly bare of vegetation, to the lowest intertidal, where they search for prey hidden by marine algae (Hartwick 1973, 1974; Groves 1982; pers. obs.). No detailed study of the food habits of this species has been made in the Strait of Georgia. A list of species taken on Cleland Island, off the west coast of Vancouver Island, shows that oystercatchers take a variety of intertidal organisms (Table 5). According to Hartwick (1974), mussels (*Mytilus*) and limpets (*Acmaea* and *Collisella*) are the major prey species. Campbell (1966) and Butler and Kirbyson (1979) reported on birds feeding on Pacific oysters (*Crassostrea gigas*) on Mitlenatch Island in the Strait of Georgia. Butler and Kirbyson (1979) found that the oystercatchers opened oysters by chipping a small hole through one of the oyster's valves and severing or paralyzing the adductor muscle.

Table 5
Prey species of the American Black Oystercatcher on Cleland Island (modified from Hartwick 1973)

Phylum	Species
Mollusca	*Mytilus edulis* *Acmaea mitra* *Collisella digitalis* *C. pelta* *Notoacmea scutum* *Crepidula nummaria* *Katharina tunicata* *Tonicella lineata* *Mopalina muscosa*
Annelida	*Nereis vexillosa* *Sipuncula* Unidentified
Echinodermata	*Cucumaria*
Arthropoda	*Petrolisthes cinctipes* *Oedignathus inermis* *Idotea* *Ligia pallasii* *Megalorchestia californiana*

Once the oyster was partly open, the oystercatcher extracted the oyster's soft body through the gap. Nine was the largest number of oysters found to be eaten in 1 h by an oystercatcher.

8. Northwestern Crow

The feeding ecology of the Northwestern Crow has been studied on Mitlenatch Island in the northern end of the Strait of Georgia. Mitlenatch Island is a 35-ha, sparsely vegetated island (Brooke *et al.* 1983) that supports about 65 breeding pairs of crows. There are two major beaches on the island where most of the crows forage. Northwest Bay beach is about 200 m long and is covered by algae from the lowest tide line to about the 2.5-m tide line, from which loose gravel extends to the highest tide line. Camp Bay beach, directly opposite Northwest Bay, is made up of mostly mud, sand, and gravel (see Richardson 1984 for a detailed description). Prey availability data were collected on Mitlenatch Island during 19 May – 30 August 1976, 27 April – 26 August 1977, and 28 April – 19 July 1978. A review of the literature and unpublished data shows that crows fed mostly on intertidal organisms and meadow invertebrates (Table 6).

8.1. Sampling methods

The seasonal availability of foods to crows in two areas—beach and meadow—was sampled in the following way:

(1) *Beach food*—To quantify the seasonal abundance of major prey items on the beach, we made weekly counts of known (Butler 1974) or suspected (pers. obs.) prey species found in a 1-m^2 plot placed at five sites chosen randomly along each of the 1-m and 3-m tide lines in Northwest and Camp bays between 28 April and 19 July 1978. The numbers of food items in the 20 plots counted each week on the beaches were then summed to provide a week-by-week index of food abundance.

(2) *Meadow food*—Meadow invertebrates were sampled in the large meadow between Northwest Bay and Camp Bay by sweep netting an approximately 1.5 m × 250 m swath once per week at midday on warm, calm days from April to July 1977–78. In addition, 10 pit traps (10 cm [diameter] × 14 cm) were opened from dawn to dusk on sweep-netting days. All invertebrates were identified to at least the family level, and only those found in nestling crow diets (Butler 1980) or regurgitated pellets (Butler 1974) or observed as prey were included in this analysis. Sweep-net and pit-trap samples were summed and provided a weekly index of food abundance in the meadows.

Table 6
Intertidal organisms found in the diet of the Northwestern Crow feeding on Mitlenatch Island (from Butler 1974, 1980; James and Verbeek 1983, 1984; Richardson 1984)

Phylum	Species
Annelida	*Nereis*
Mollusca	*Venerupis japonica* *Protothaca staminea* *Macoma nasuta* *Saxidomus giganteus* *Clinocardium nuttallii* *Mytilus edulis* *Crassostrea gigas* *Littorina sitkana* *Thais lamellosa* *Lepidozona cooperi* *Tonicella lineata*
Crustacea	*Pugettia producta* *Cancer productus* *C. magister* *Hemigrapsus nudus* *H. oregonensis* *Callianassa* *Spirontocaris*
Chordata	*Anoplarchus purpurescens* *Clinocottus* *Liparis*

To examine whether the beach or meadow was the preferred foraging site during low tides, we recorded the origin of feeding bouts of males and females after leaving the nest. The exposed beach was divided along the 2.5-m tide line, and we recorded the number of feeding bouts in the meadow and on the beach when only the upper half (2.5- to 4.0-m tides) of the beach was dry and when the lower half (0.0- to 2.5-m tides) of the beach was exposed. We predicted that as the tide dropped more crows would use the beach than the meadows.

Nests were visited at least once per week once the first egg was laid, and the contents were recorded to relate the timing of nesting with food abundance. We used pipe-cleaner collars on nestling crows to sample food fed by adults. Fourteen pairs of crows were watched for 3477 min to record the amount of time devoted to feeding on the beach and meadow through the nesting season. Observations were made through binoculars and telescope from a vantage point on a hill about 200 m from their nests. Movements were noted into a tape-recorder and transcribed later.

8.2. Spatial and temporal distribution of major prey

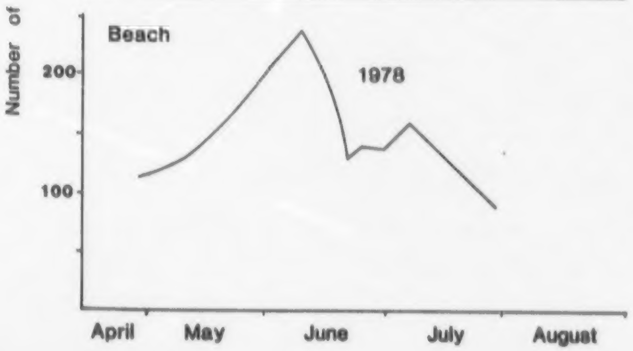
On Northwest Bay beach, we found mostly shorecrabs (*Hemigrapsus nudus* and *H. oregonensis*; 58.4%) and cockscomb pricklebacks (*Anoplarchus purpurescens*; 12.2%) among 188 food items in weekly plots. In Camp Bay, shorecrabs, littleneck clams (*Venerupis staminea*), and cockscomb pricklebacks totaled 1478 (74.4%), 306 (15.4%), and 38 (1.9%), respectively, of 1987 prey items found in weekly plots. Butler (1980) found that clams (27.9%), crabs (21.5%), and pricklebacks (15.2%) were the three food items most frequently fed to 53 nestling crows on Mitlenatch Island. Shorecrabs and littleneck clams were most abundant in the 3.0-m tidal zone (Ricketts and Calvin 1968), and pricklebacks were most often found lower on the beach around the 1.0-m tide line (Lamb and Edgell 1986). Very few prey items occurred in the loose gravel along the 3.0-m tide line in Northwest Bay, but clams and crabs flourished in Camp Bay. Invertebrates ($n = 1085$) captured during sweep netting and pit trappings in the meadows included the taxonomic orders Homoptera (52.1%), Arachnida (28.0%), Coleoptera (6.0%), Diptera (4.7%), Hemiptera (4.3%), Hymenoptera (3.1%), and Lepidoptera (1.8%). All those groups were represented in the 53 samples of nestling food but in a different order of abundance. Arachnida occurred most frequently (36.0% of the samples), followed by Lepidoptera (20.0%), Coleoptera (12.0%), Diptera (10.0%), Homoptera and Hymenoptera (8.0% each), and Hemiptera (4.0%). Orthoptera, which was not found in sweep-netting and pit-trapping samples, occurred in 2.0% of the nestling food samples.

Beach and meadow food items increased numerically from April to June and then decreased through July (Fig. 2). The June peak in abundance coincided with the longest days and the lowest diurnal tides of the year (Butler 1980).

8.3. Availability of prey

In the Strait of Georgia, tides are mixed semidiurnal, so that in a 25-h cycle there are two high and two low tides (LeBlond, this publication). In addition, the daytime tides become progressively lower until early June and then revert to increasingly higher diurnal tides. As a result, littleneck clams and shorecrabs (along the 3.0-m tide line) were exposed by low tides at least once a day from April to September during this study, but pricklebacks (at the 1.0-m tide line) were exposed on only 2 d in April, 6 d in May, and 7 d each in June and July. For the rest of the year, the crows could not reach the pricklebacks. Furthermore, the crows could hunt for shorecrabs and littleneck clams for up to 8.5 h between tides compared with no more than 1 h for pricklebacks.

Figure 2
Seasonal food abundance of meadow invertebrates, intertidal beach organisms, and the nestling season of Northwestern Crows on Mitlenatch Island (narrow lines = one quartile; wide line = one interquartile)



8.4. Foraging in relation to availability of prey

The crows preferred to forage on the beach when given a choice. When the prickleback zone (1.0-m tide line) was exposed, significantly ($P < 0.001$) more foraging bouts began on the beach ($n = 14$) compared with the meadows ($n = 5$) than when only the crab and clam zone (3.0-m tide line) was exposed (beach = 7, meadow = 33; $\chi^2 = 7.3$, df = 1). Richardson (1984) showed that crows chose the prickleback zone, whenever it was dry, over the clam and crab zone higher on the beach. In addition, we found significantly ($P < 0.01$) more crows on the beach when pricklebacks were available ($\bar{x} = 10.5$, SD = 6.1, $n = 36$) than when only crabs and clams were available ($\bar{x} = 7.8$, SD = 7.1, $n = 16$; $t = 3.45$, df = 50).

The beaches on Mitlenatch Island constitute about one-fifth of the land area available to crows during the lowest tide, but the crows spent 44.0–60.1% of their time foraging there (Table 7). During the breeding season (May and June), the 3.0-m tide line is exposed for about 8.5 h (53.1%) of the 16 h of daylight, which is very similar to the amount of time the crows devoted to foraging there (49.9%; Table 7). Clearly, the crows preferred to forage on the beaches over the meadows during low tides.

8.5. The relationship between breeding biology and food

Crows from all parts of the island fed on the beaches. We expected that pairs holding beach edge territories might lay larger clutches, lose fewer eggs to predators, and raise more offspring than more distantly nesting pairs. However, no significant differences in clutch size or the number of eggs lost occurred in nests built close to and far from the beach (Richardson *et al.* 1985). However, nests near the beach fledged significantly more young than more distantly located nests. Richardson *et al.* (1985) suggested that food provisioning was the likely cause of high nestling loss in distantly located nests. Most nests in territories adjacent to the beach were about 50 m from the intertidal zone, whereas distantly located nests were up to 250 m inland. Although that is only a 200-m difference, when multiplied by the 1460 trips flown to feed nestlings (Butler 1980), pairs nesting near the beach flew 73 km, and pairs farther inland flew 365 km, to raise their young. The extra time and effort required to fly to the beach might have meant longer bouts away from distantly located nests, which resulted in less provisioning for those young.

The cyclic nature of the oceanic tides not only affects the daily comings and goings of foraging crows, but also appears to determine when the crows will nest. The greatest food demands imposed upon the parents during the nesting season presumably occur when the nestlings are growing most rapidly. It would make sense for adult crows to time their nesting season to coincide with the

Table 7
Percentage of time ($n = 3477$ min of observation) spent foraging on the beach and meadow by 14 pairs of crows in 1977–78

Nesting stage	Beach	Meadow
Egg	44.0	56.0
Nestling	60.1	39.9
Fledgling[a]	45.6	54.4
Mean	**49.9**	**50.1**

[a] Up to 17 d following nest departure by the nestlings.

maximum amount of available food. Most nestlings were present in early June during the lowest daytime tides of the year and when the days were longest and the greatest number of beach invertebrates were present (Fig. 2).

Several studies have shown that the crows on Mitlenatch Island eat mostly foods gleaned from the intertidal beach (Butler 1974; James and Verbeek 1983, 1984; Richardson 1984). Although several thousand Glaucous-winged Gulls (*Larus glaucescens*) and hundreds of Pelagic Cormorants (*Phalacrocorax pelagicus*) and Pigeon Guillemots (*Cepphus columba*) also nest on the island, they do not seem to supply much food to most crows. In the Strait of Georgia, Mandarte, Snake, Vivian, and Christie islands support seabirds and small to moderate populations of breeding crows. However, not all of those crows rely heavily on beach food. Verbeek (1982) showed that crows on Mandarte Island ate large numbers of seabird eggs, mostly during disturbances. Elsewhere in the Strait of Georgia, crows nest several kilometres away from the seashore where beach food is unavailable. In other coastal environments, Northwestern Crows mainly scavenge seabird colonies for food dropped by nocturnal alcids and avoid the beach (Butler *et al.* 1985). Clearly, the crow is highly adapted to take advantage of opportunities to find food. Under normal conditions, crows seem to coexist with other birds on the BC coast, but during disturbances to seabirds they can quickly tip the balance in their favour. This does not suggest a crow control program is needed. Instead, it reinforces the need to limit human disturbances in and around seabird nesting sites.

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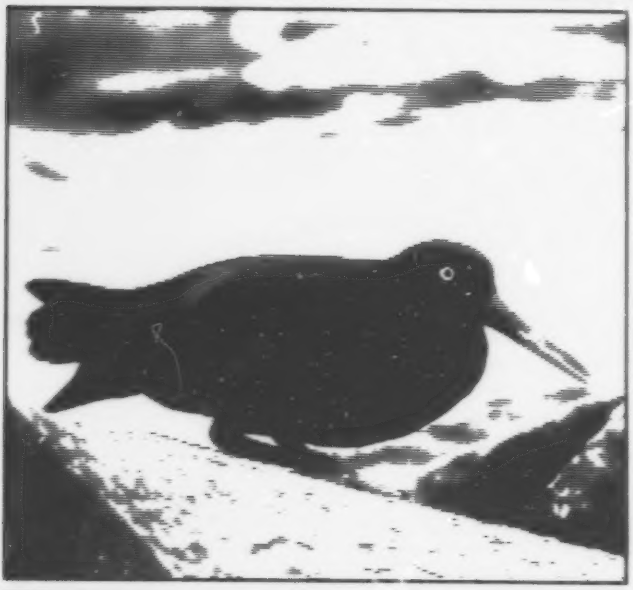
Part 3

Populations and breeding ecology of marine birds



Introduction to the nesting seabirds of the Strait of Georgia

Kees Vermeer

1. Abstract

The status and biology of nesting seabirds in the Strait of Georgia are reviewed. The numbers of such birds have vastly increased since Drent and Guiguet (1961) made their first inventory in 1959–60. There has also been a small change in species composition of these birds during the past few years. A comparison of the populations of nesting seabirds in the Strait of Georgia with those elsewhere on the BC coast shows that there is less species diversity in the strait. Possible explanations for these differences are given. It is recommended that researchers:
(1) monitor the establishment of new species in the Strait of Georgia;
(2) conduct an inventory of physical and biological factors affecting the distribution of island-nesting seabirds;
(3) sample fishes and plankton in surface waters where seabirds are feeding to determine relationships of these prey organisms to those observed in the bird diet; and
(4) collect baseline information on the distribution and numbers of Marbled Murrelets (*Brachyramphus marmoratus*).

2. Résumé

L'auteur étudie la situation et la biologie des oiseaux marins nicheurs du détroit de Georgia. Les populations de ces oiseaux ont considérablement augmenté depuis que Drent et Guiguet (1961) ont dressé leur premier inventaire en 1959 et 1960. Au cours des dernières années, le nombre d'espèces a quelque peu changé. Si l'on compare les populations d'oiseaux marins nicheurs dans le détroit de Georgia et celles qui vivent ailleurs sur la côte de la Colombie-Britannique, on s'aperçoit qu'il y a moins d'espèces différentes dans le détroit. L'auteur propose des explications possibles de ces différences. Il est recommandé que les chercheurs:
(1) surveillent l'introduction de nouvelles espèces dans le détroit de Georgia;
(2) dressent une liste des facteurs physiques et biologiques qui influent sur la distribution des oiseaux marins qui nichent dans l'île;
(3) prélèvent des échantillons de poissons et de plancton dans les eaux de surface où les oiseaux marins s'alimentent afin d'établir des rapports entre ces proies et celles observées dans l'alimentation des oiseaux;
(4) recueillent des données de base sur la distribution et la population des Alques marbrées (*Brachyramphus marmoratus*).

3. Background and present status

Seven species of seabirds are known to nest on islands in the Strait of Georgia: the Glaucous-winged Gull (*Larus glaucescens*), Pelagic Cormorant (*Phalacrocorax pelagicus*), Double-crested Cormorant (*P. auritus*), Brandt's Cormorant (*P. penicillatus*), Pigeon Guillemot (*Cepphus columba*), Rhinoceros Auklet (*Cerorhinca monocerata*), and Tufted Puffin (*Fratercula cirrhata*). An eighth species, which commonly occurs in the strait and undoubtedly nests along its shores, is the Marbled Murrelet (*Brachyramphus marmoratus*).

The four most numerous island nesters in the Strait of Georgia are the Glaucous-winged Gull, the Pelagic and Double-crested cormorants, and the Pigeon Guillemot. The Glaucous-winged Gull, which is the best-studied seabird in the strait, is the only gull that nests in the strait, although another dozen larid species visit the region. Its breeding biology (Vermeer 1963; Ward 1973; Hunt and Hunt 1976; Verbeek 1986), dispersal and postfledging mortality (Pearse 1963; Butler *et al.* 1980), and nest site selection (Vermeer and Devito 1987) have been examined in detail. Vermeer and Devito discuss the present status and population trend of this gull in the next paper.

Aspects of the nesting biology and behaviour of Pelagic and Double-crested cormorants have been studied by Drent *et al.* (1964), Robertson (1971), and Siegel-Causey and Hunt (1981). Recent population trends of the two species were investigated by Vermeer and Rankin (1984). Vermeer, Morgan, and Smith report on the present population trends of the cormorants in the third paper in Part 3.

The nesting behaviour and biology of the Pigeon Guillemot have previously been investigated on Mandarte Island in the southern Strait of Georgia (Drent 1965). In the last paper in Part 3, Emms and Morgan report on the nesting biology of the species on Mitlenatch Island in the northern Strait of Georgia, as well as on its distribution throughout the strait.

Of the three species that nest in very small numbers in the Strait of Georgia, the Brandt's Cormorant (three pairs) has been reported as nesting on Race Rocks at the junction of the Straits of Georgia and Juan de Fuca in 1987 (Anon. 1988); the Rhinoceros Auklet (about six pairs) has been reported as nesting on Mandarte Island in 1986 (P. Arcese, pers. commun.); and the Tufted Puffin (one or two pairs) has nested for many years on Mandarte Island (Drent and Guiguet 1961).

Little is known about the past and present nesting and population status of the Marbled Murrelet in the Strait of Georgia. Sealy and Carter (1984) reported on the at-sea distribution and the nesting habitat of the Marbled Murrelet in British Columbia.

4. General nesting biology

The nesting biology of the four seabird species that commonly breed in the Strait of Georgia is briefly dealt with here. As for the three less-common nesting species in the strait, the reader is referred to the following studies: the nesting biology of the Rhinoceros Auklet has been studied on the outer coast of British Columbia (Vermeer 1979, 1980; Vermeer and Westrheim 1984) and on the American side of the Strait of Juan de Fuca (Wilson and Manuwal 1986); that of the Tufted Puffin has been examined on the west coast of British Columbia (Vermeer 1979; Vermeer *et al.* 1979); and that of the Brandt's Cormorant has been studied in California (Boekelheide and Ainley 1988).

Glaucous-winged Gulls nest, either solitarily or in colonies up to 2300 pairs, on islands throughout the Strait of Georgia. They usually nest on the grass substrate of small to moderate-sized islands; however, they also nest on barges, beacons, bridge supports, cliff ledges, derricks, log booms, and pilings, as well as in cliff cavities. Glaucous-winged Gulls recently started to nest in large numbers on roofs of buildings in coastal cities (Vermeer and Devito 1987; Vermeer *et al.* 1988; Hooper 1988). Glaucous-winged Gulls are thus very plastic in their choice of nesting habitat. On islands in the strait, their nests are located mostly in the open and consist of grass. Usually three eggs are laid at an average interval of 55 h. Incubation averages 27 d. The young are raised over a 44-d period (mean age at first flight) and leave their colonies at 48–65 d of age (Vermeer 1963). The nesting season—the interval from the laying of the first egg until the fledging of the last young—can last from about the second week of May until the end of August.

Double-crested and Pelagic cormorants nest chiefly in colonies. The Double-crested Cormorant is restricted to the southern portion of the Strait of Georgia, whereas the Pelagic Cormorant is found throughout the strait. The Double-crested Cormorant nests mostly on the ground, but also on dolphins and in trees; the Pelagic Cormorant nests mostly on cliff ledges, but also on the ground and on bridge supports (Vermeer, Morgan, and Smith, Part 3, this publication). For building nests, Double-crested Cormorants use chiefly branches, whereas Pelagic Cormorants use mostly grass. Usually four eggs are laid, but Double-crested and Pelagic cormorants may lay up to five and six eggs, respectively. Incubation for the Double-crested Cormorant averages 28 d, and that for the Pelagic Cormorant, 31 d (Drent *et al.* 1964). Young Double-crested and Pelagic cormorants leave the nests when seven to eight weeks of age. The nesting season of the Double-crested Cormorant lasts from the end of April until well into September. Most clutches are laid in May, but second and replacement clutches may be started as late as August. Young may still be raised from these late layings (Drent and Guiguet 1961). The nesting season of the Pelagic Cormorant starts later than that of the Double-crested Cormorant and lasts from the end of May until September.

Pigeon Guillemots generally nest in loose colonies on islands throughout the Strait of Georgia. Their nests are found in cavities or cracks in rocks, in chambers in the soil below rock slabs, and also in abandoned burrows of other animals. Usually two eggs are laid 3 d apart. Incubation averages 30 d, and chicks leave the nest when about 35 d old (Drent 1965). The nesting season of the Pigeon Guillemot lasts from the latter half of May until the end of August.

5. Comparison between the Strait of Georgia and the outer BC coast

The importance of the seabird population in the Strait of Georgia is compared on a numerical and percent basis with that on the BC coast outside the strait (hereafter referred to as the "outer coast") in Table 1. Of a total nesting population of at least 5 000 000 seabirds in British Columbia, the Strait of Georgia portion constitutes less than 1%. In the strait, the Glaucous-winged Gull is by far the most numerous nesting seabird (71.2%); on the outer coast, it is unimportant (0.6%) in comparison with other species (Table 1). The Glaucous-winged Gull population is rapidly increasing in the strait (Vermeer and Devito, this publication). The population increase may relate to an abundant supply of human refuse on which these gulls feed (Vermeer 1963; Butler *et al.* 1980; Vermeer and Devito, this publication). Glaucous-winged Gulls feed extensively on refuse in the strait but do so much less on the outer coast (Vermeer 1982).

The greater species diversity outside the Strait of Georgia than within it (Table 1) may reflect the presence of certain foods, as well as the absence or scarcity of feeding and nesting habitats in the strait. The Cassin's Auklet (*Ptychoramphus aleuticus*) is by far the most numerous breeding seabird in British Columbia (about 48% of the total nesting population) but does not appear to nest in the strait. Cassin's Auklets feed mostly on zooplankton over the continental shelf, banks, and seamounts of the outer coast during the breeding period (Vermeer 1981; Vermeer *et al.* 1985). Their main prey is the copepod *Neocalanus cristatus*, which is scarce or absent in the Strait of Georgia (J. Fulton, pers. commun.). The Fork-tailed Storm-Petrel (*Oceanodroma furcata*), like the Cassin's Auklet, forages chiefly over the shelf and shelf break of the outer coast,

Table 1
Comparison of currently (1988) estimated breeding populations of marine birds in the relatively sheltered waters of the Strait of Georgia and in the exposed waters on the BC outer coast

Species	Strait of Georgia[a] No.	Strait of Georgia[a] %	BC coast outside the strait[b] No.	BC coast outside the strait[b] %
Storm-petrels (Fork-tailed and Leach's)	–	–	1 526 234	29.2
Brandt's Cormorant	6	Trace	126	Trace
Double-crested Cormorant	4 000	11.0	–	–
Pelagic Cormorant	4 700	12.9	3 700	0.1
Glaucous-winged Gull	26 000	71.2	30 000	0.6
Common Murre	–	–	5 620	0.1
Thick-billed Murre	–	–	70	Trace
Pigeon Guillemot	1 800[c]	4.9	8 400	0.1
Ancient Murrelet	–	–	543 000	10.4
Cassin's Auklet	–	–	2 354 000	45.1
Rhinoceros Auklet	12	Trace	680 000	13.0
Tufted Puffin	4	Trace	77 000	1.5
Horned Puffin	–	–	50	Trace
Total no. of birds	**36 522**		**5 228 200**	

[a] Vermeer and Devito; Vermeer, Morgan, and Smith, Part 3; Emms and Morgan; this publication.
[b] M. Rodway, pers. commun.
[c] Estimated.

whereas the Leach's Storm-Petrel (*O. leucorhoa*) feeds far offshore and in warm oceanic currents during summer (Vermeer and Rankin 1984). Both storm-petrel species feed extensively on the amphipod *Paracallisoma coecus* and on myctophid fishes (Vermeer and Devito 1988), which are deep-water organisms and are scarce or absent in the strait. The lack of suitable nesting habitat for burrow-nesting seabirds and the presence of numerous Glaucous-winged Gulls in the strait may also limit species such as Cassin's Auklets and Fork-tailed and Leach's storm-petrels. Glaucous-winged Gulls can prey extensively on small alcids and storm-petrels (Trapp 1979).

It is interesting that the few Rhinoceros Auklets and Tufted Puffins nesting in the Strait of Georgia are found on Mandarte Island, which is not far from the exposed waters of the Strait of Juan de Fuca. A large colony of Rhinoceros Auklets is found on Protection Island, and a small one on Smith Island, both at the eastern end of the Strait of Juan de Fuca (Wilson and Manuwal 1986). This may indicate that Rhinoceros Auklets prefer to nest near exposed waters. Vermeer (1979) suggested that the nesting distribution of Rhinoceros Auklets and Tufted Puffins is determined by both food supply and suitable nesting habitat. Another factor limiting the presence of Tufted Puffins may be predation. Puffins are extensively kleptoparasitized by Glaucous-winged Gulls on Triangle Island on the outer coast (Vermeer 1979).

Common Murres (*Uria aalge*) may not nest in the Strait of Georgia because of a lack of appropriate nesting conditions. Although there are a number of islands with suitable nesting cliffs in the strait, the murres would be susceptible there to frequent human disturbance and to predation by domestic mammals and river otters (*Lutra canadensis*). River otters have been observed to prey extensively on Glaucous-winged Gull colonies in the strait (Foottit and Butler 1977; Verbeek and Morgan 1978; Vermeer and Devito, this publication).

Ancient Murrelets (*Synthliboramphus antiquus*) do not nest in the Strait of Georgia. They are apparently restricted to nesting mostly in the Queen Charlotte Islands in northern British Columbia. The species may breed on these islands because of their offshore location and their open habitat beneath mature forest (Vermeer and Lemon 1986). Forested islands in British Columbia away from the Queen Charlotte Islands generally have a dense understory of shrubs (Pojar and Banner 1984).

The Double-crested Cormorant occurs only in the southern portion of the Strait of Georgia and does not nest elsewhere on the BC coast (Table 1). However, in Washington State, Double-crested Cormorants commonly breed on both the inner and outer coasts (Manuwal and Campbell 1979).

6. Recommendations for future studies

There has been a recent and dramatic increase in the seabird numbers in the Strait of Georgia (cf. Drent and Guiguet 1961; papers in Part 3). The effect of these changes on the strait's ecosystem is unknown. However, the population of Bald Eagles (*Haliaeetus leucocephalus*), whose main prey in the Gulf Islands is the Glaucous-winged Gull, is known to have increased subsequently (Vermeer, Morgan, Butler, and Smith, this publication). The reproductive success of American Black Oystercatchers (*Haematopus bachmani*) may be negatively affected by the expanding population of gulls (Vermeer, Morgan, and Smith, Part 3, this publication).

Besides the increase in seabird numbers, there has been a very recent and small change in the species composition of nesting seabirds in the Strait of Georgia. The appearance of Brandt's Cormorants (first observed in 1987) and Rhinoceros Auklets (first observed in 1986) in the most southern portion of the strait may signify changes in prey abundance or availability in surface waters, human disturbance or predation on nesting islands in adjacent waters outside the strait, or other unknown factors. Whatever the reason for the birds' appearance in the strait, their possible expansion, and that of any yet to be discovered species in the strait, should be closely observed and monitored.

As previously suggested, a lack of suitable nesting habitat may explain the absence or scarcity of burrow-nesting species. More quantitative data, however, are necessary to confirm this hypothesis. A thorough inventory of both physical (e.g., the presence and depth of soil for burrowing) and biological (e.g., relative openness of terrain; presence of predators such as cats, dogs, mink, rats, river otters, and garter snakes; extent of human disturbance) factors should be carried out for all islands in the Strait of Georgia.

We know little about the size and distribution of the nesting population of Marbled Murrelets in the Strait of Georgia. Because nest sites are difficult to locate, shoreline surveys of murrelet numbers during the breeding period would provide baseline data on the distribution and the approximate size of the murrelet population. Murrelet distribution should be related to different types of coastal forests, as the birds nest solitarily in forested areas mostly within 20 km of the sea (Paton *et al.* 1988). Obtaining information of this nature is only the first step to understanding the niche that the Marbled Murrelet occupies in the strait. The next step would be to census murrelets at inland stands of old-growth forests, as these birds commonly use such stands for nesting (for census methods, see Paton *et al.* 1988). Other forested areas within about 20 km of the seashore should also be investigated to determine the presence of murrelets.

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Population trend of nesting Glaucous-winged Gulls in the Strait of Georgia

Kees Vermeer and Kevin Devito

1. Abstract

The nesting population of Glaucous-winged Gulls (*Larus glaucescens*) was censused in the Strait of Georgia in 1986, and the reproductive success of small and large colonies was investigated. In 1986, 13 000 nesting pairs were found. The gull population has doubled since 1960. Large colonies produced more fledglings (1.1–1.4 per nest) than did small colonies (0.3 per nest). The low reproductive success of small colonies has apparently been caused by predation. Bald Eagles (*Haliaeetus leucocephalus*), Northwestern Crows (*Corvus caurinus*), and river otters (*Lutra canadensis*) were observed to prey on gulls.

2. Résumé

La population de Goélands à ailes grises (*Larus glaucescens*) qui nichait a été recensée dans le détroit de Georgia en 1986, et le succès de la reproduction dans les petites et les grandes colonies a été étudié. En 1986, 13 000 couples d'oiseaux nicheurs ont été observés. La population de Goélands à ailes grises a doublé depuis 1960. Les grandes colonies ont produit plus d'oisillons (1,1–1,4 par nid) que les petites colonies (0,3 par nid). Le faible succès de la reproduction dans les petites colonies a apparemment été causé par la prédation. On a observé que l'Aigle à tête blanche (*Haliaeetus leucocephalus*), la Corneille du Nord-Ouest (*Corvus caurinus*) et la Loutre de rivière (*Lutra canadensis*) s'attaquaient aux goélands.

3. Introduction

Drent and Guiguet (1961) conducted the first survey of Glaucous-winged Gulls (*Larus glaucescens*) in the Strait of Georgia in 1959 and 1960 by conducting nest counts and by corresponding with naturalists and lightkeepers who possessed information on individual colonies. Campbell (1976) censused gull colonies in the Strait of Georgia in 1974 and 1975 and displayed the survey results in a wall map of seabirds of the Vancouver Island area. Campbell's (1976) census showed that the gull population in the strait had increased since 1959 and 1960. Vermeer (1963) investigated the reproductive success and adult survival of Glaucous-winged Gulls on Mandarte Island, a colony with 2200 breeding pairs (Fig. 1). Butler *et al.* (1980) constructed a life table based on 1002 recoveries of chicks banded in 11 colonies in southern British Columbia.

We conducted a census of nesting sites of Glaucous-winged Gulls in the Strait of Georgia in 1986 to determine if the gull population had further increased since Campbell's (1976) census. We also investigated the reproductive success for solitary pairs and small and large colonies in the Gulf Islands in 1985 and 1986, and on the Chain Islands in 1986, to determine if reproductive success varied with colony size. Past and present growth rates of the Glaucous-winged Gull population in the Strait of Georgia were estimated.

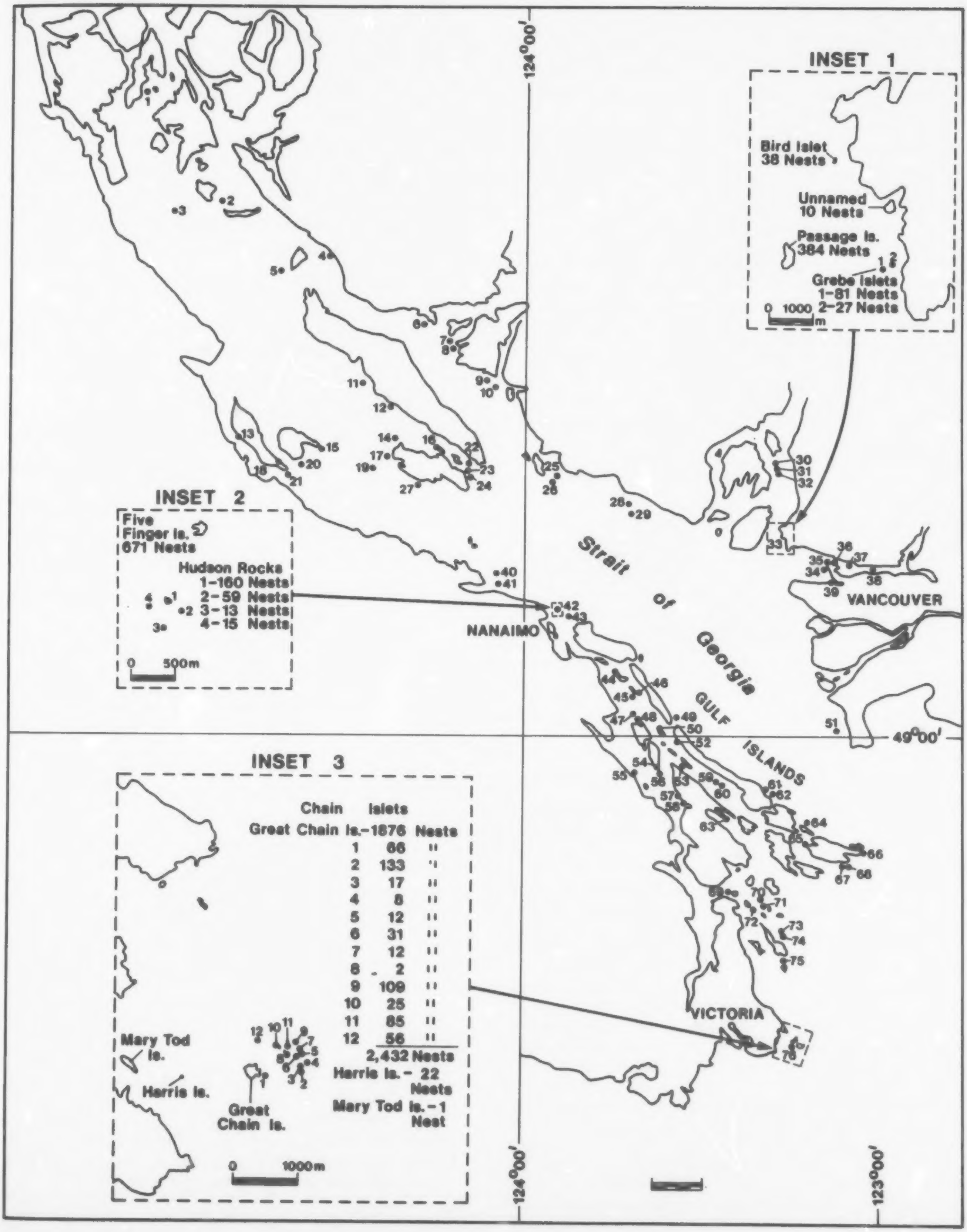
4. Methods

We censused gulls at nesting sites in the Strait of Georgia during the period 6 June – 24 June 1986. Observers landed on islands and conducted the census by walking systematically through colonies and counting nests. Where cormorants were present, nests or nesting pairs of gulls were counted from a distance on land or from a boat to prevent disturbing nesting cormorants. The numbers of nests or nesting pairs on beacons, bridges, cliffs, and pilings were counted from the boat itself. Small to moderate-sized colonies were censused once or twice by one or two observers. When censused twice, counts were averaged. A group of four to six observers censused the large colonies on Chain, Mandarte, and Mitlenatch islands. Small to moderate-sized colonies could be censused within 1 h, but large colonies took 1 d each. Counts in the three large colonies were conducted in strips marked by stakes and string to prevent double-counting of nests or missing colony sections. Although it is unlikely that any large or moderate-sized colony was missed, some small colonies (2–50 nests) may have been overlooked, and many solitary pairs were undoubtedly missed during the census. Because solitary pairs and small colonies make up only a very small fraction of the total population, we think that the 1986 census provides a reasonably accurate estimate of the total nesting population in the Strait of Georgia. Not included in the 1986 census were the many gulls nesting on roofs of buildings in the cities and towns bordering the strait (Vermeer *et al.* 1988).

Our methods differ from those of Drent and Guiguet (1961) in that we counted nests at sites, whereas much of Drent and Guiguet's (1961) census was done by correspondence. Campbell (1976) censused colonies, but the author did not provide census methods.

The survival of Glaucous-winged Gull chicks was investigated for solitary pairs and nesting pairs in different-sized colonies on the Gulf Islands in 1985–86 and on the Chain Islands in 1986. Nests were counted in those colonies from 6 to 24 June, and fledglings, or chicks

Figure 1
Distribution of Glaucous-winged Gull nesting sites found in 1986 in the Strait of Georgia. Numbered colonies are identified in Table 1.


124°00′
49°00′
123°00′
Strait of Georgia
GULF ISLANDS
VANCOUVER
NANAIMO
VICTORIA
INSET 1
Bird Islet
38 Nests
Unnamed
10 Nests
Passage Is.
384 Nests
Grebe Islets
1-81 Nests
2-27 Nests
0 1000 m
INSET 2
Five Finger Is.
671 Nests
Hudson Rocks
1-160 Nests
2-59 Nests
3-13 Nests
4-15 Nests
0 500m
INSET 3
Chain Islets
Great Chain Is.-1876 Nests
1 66 "
2 133 "
3 17 "
4 8 "
5 12 "
6 31 "
7 12 "
8 2 "
9 109 "
10 25 "
11 85 "
12 56 "
2,432 Nests
Harris Is.- 22 Nests
Mary Tod Is.-1 Nest
Mary Tod Is.
Harris Is.
Great Chain Is.
0 1000m

approaching fledging age, were counted at the same sites from 4 to 12 August. The reproductive success on Mandarte Island was calculated by counting all nests and fledglings on meadow A at the northeastern tip of the island, which is distinctly separated by shrubbery and a small valley from other subcolonies (Vermeer 1963). A subjective census of fledglings on other portions of Mandarte Island suggested that fledging rates there were similar to those on meadow A. The reproductive success on Great Chain Island was estimated from selected subsamples of the entire colony.

5. Results

We counted a total of 13 002 nests of Glaucous-winged Gulls on nesting sites in the Strait of Georgia in 1986 (Table 1). Glaucous-winged Gulls nested on many islands, beacons, cliffs, and pilings throughout the strait, but the largest nesting concentrations were found in the southeastern portion on the Chain and Gulf islands (Fig. 1). Although solitary nesting pairs and small colonies (2–50 pairs) made up 68.5% of the nesting localities, they constituted only 5.5% of the nesting population (Table 2). Almost half (47.9%) the nesting population occurred on three islands: Great Chain, Mandarte, and Mitlenatch.

The reproductive success or fledging rate of Glaucous-winged Gulls in the Chain and Gulf islands is shown in Table 3. The fledging rate on Mandarte Island was estimated to be 1.4 fledglings per nest in both 1985 and 1986. Smaller colonies in the Gulf Islands averaged about 0.3 fledglings per nest in 1985 and 1986. The fledging rate on Mandarte Island was therefore about five times higher than in the smaller colonies. The average fledging rate on islets with small colonies in the Chain Islands was estimated to be 1.1 fledglings per nest, and that on Great Chain Island about 1.0–1.5 fledglings per pair. The rate on the small Chain Islands is considerably higher than that observed for solitary pairs and small colonies in the Gulf Islands, perhaps because all the Chain Islands are very close to one another (Fig. 1) and can be considered as one colony. Fledging rates show that the large Mandarte and Chain islands colonies had much higher reproductive success than did the solitary nesting pairs or the small to moderate-sized colonies in the Gulf Islands.

6. Discussion

6.1. 1960–86 population trends

The population growth of Glaucous-winged Gulls is shown for two of the three largest colonies in the Strait of Georgia in Figure 2. Mandarte Island represents the southern half and Mitlenatch Island the northern half of the strait. The Mandarte population increased from 1915 to the early 1960s, at which time the population leveled off, presumably because all the available and suitable nesting habitat on the island meadows was utilized (KV, pers. obs.). At present, many gulls have started to nest on the upper portion of the rocky beach habitat of the island; only a few nested there in the 1960s. The nesting population of gulls on Mitlenatch Island appears to be still increasing, perhaps as much of the nesting habitat on that island is still unutilized by gulls (pers. obs.). The rapid growth rate and early leveling off of the gull population on Mandarte Island, compared with that on Mitlenatch Island, may be related to the fact that Mandarte Island is near large human refuse dumps in the much more human-populated

Table 1
Nesting distribution of Glaucous-winged Gulls in the Strait of Georgia in 1986

No.[a]	Name of nesting locality	No. of nests counted
1	Little Rock	1
2	Keefer Rock	28
3	Mitlenatch Island	2 100
4	Boat hulks, Powell River	6
5	Vivian Island	208
6	McRae Islet	262
7	Unnamed islet	1
8	Unnamed islet	1
9	Unnamed islet	1
10	Hodgson Islands	1
11	Mouat Islands	35
12	Unnamed island (Davie Bay)	3
13	Ferry Dock, Denman Island	1
14	Fegan Islets	1
15	St. John Point, Hornby Island	6
16	Unnamed islet	1
17	Finnerty Islands (rock)	4
18	Gravelly Bay Ferry Dock, Denman Island	1
19	Sisters Islets	25
20	Norris Rocks	287
21	Chrome Island	3
22	Unnamed islet	50
23	Unnamed islet	22
24	Unnamed islet	1
25	Merry Island	6
26	Franklin Island	216
27	Sea Egg Rocks	5
28	White Islets (main)	470
29	White Islets (rock)	20
30	Christie Islet	454
31	Pam Rock	96
32	Pam Rock (small)	13
33	Islands in Queen Charlotte Islands Channel (see inset)	540
34	Siwash Rock and adjacent rocks	8
35	Prospect Point	4
36	Lions Gate Bridge	1
37	Pilings, Burrard Inlet	8
38	Second Narrows Bridge	40
39	Burrard Bridge	9
40	Ada Island (rock)	124
41	Maude Island (rock)	2
42	Five Finger Island and Hudson Rocks (see inset)	918
43	Snake Island	673
44	De Courcy Island	2
45	Ruxton Island	2
46	Unnamed islet (off Ruxton)	1
47	Miami Islet	38
48	Ragged Islets	69
49	Canoe Islet	56
50	Rose Islets (see inset)	116
51	Tsawwassen breakwater	238
52	Cliffs, Galiano Island	6
53	Unnamed rocks (Wallace Island)	3
54	Cliffs and cliff cavities, Kuper Island	8
55	Cliffs, Bare Point	5
56	Cliffs and cliff cavities, Tent Island	12
57	Dock Point, Saltspring Island	1
58	Vesuvius Dock and Bay Rocks	3
59	Ballingall Islets (west)	89
60	Ballingall Islets (east)	56
61	Lion Islets	1
62	Unnamed rock, Gossip Island	1
63	Ganges and Long Harbour	6
64	Belle Chain Islets	56
65	Saturna Point, Saturna Island	1
66	East Point, Saturna Island	7
67	Java Islets (west)	132
68	Java Islets (east)	166
69	Arbutus Island	150
70	Imrie Island	216
71	Greig Island	52
72	Little Group Islands	6
73	Mandarte Island	2 259
74	South Islet (165 m SE of Mandarte)	104
75	Sallas Rocks	29
76	Chain, Mary Tod, and Harris islands (see inset)	2 455
Total no. of nests counted		**13 002**

[a] Numbers correspond to locations in Figure 1.

Table 2
Colony size of Glaucous-winged Gulls in relation to number of nesting localities and number of nests in the Strait of Georgia, 1986

No. of nests	No. of nesting localities (%)	No. of nests (%)
1	25 (23.1)	25 (0.2)
2–10	26 (24.1)	144 (1.1)
11–50	23 (21.3)	553 (4.2)
51–100	12 (11.1)	859 (6.6)
101–250	12 (11.1)	1976 (15.3)
251–1000	7 (6.5)	3210 (24.7)
1001–2500	3 (2.8)	6235 (47.9)

Table 3
Comparison of fledging rates of Glaucous-winged Gulls on Mandarte Island and other nesting locations in the Gulf Islands in 1985 and 1986, and on the Chain Islands in 1986

	Colony size (no. of nests)		No. of fledglings		Fledging rate (no. of fledglings/nest)	
Nesting locality	**1985**	**1986**	**1985**	**1986**	**1985**	**1986**
Mandarte Island	2157	2259	–	–	1.4 (est.)	1.4 (est.)
Meadow A	90	128	125	182	1.39	1.42
Other Gulf Islands						
Arbutus Island	115	190[a]	80	2	0.70	0.01
Ballingall Islets (west)	–	89	–	20	–	0.22
Ballingall Islets (east)	37	56	16	0	0.43	0
Canoe Islet	–	56	–	32	–	0.57
Creig Island	45	52	28	17	0.62	0.54
Cliffs, Galiano Island	6	6	5	0	0.83	0
Cliffs and cliff cavities, Kuper Island	–	8	–	3	–	0.38
Cliffs and cliff cavities, Tent Island	11	12[a]	0	0	0	0
Imrie Island	120[b]	216	0	120	0	0.55
Java Islets (2 islets)	–	298[b]	–	170	–	0.57
Miami Islet	–	38	–	20	–	0.53
Rose Islets (3 islets)	112	116[a]	40	0	0.36	0
Ragged Islets (1 islet)	–	69[a]	–	0	–	0
South Islet	100[a]	104[a]	0	5	0	0.05
Unnamed rocks, Wallace Island	3	3[b]	2	0	0.67	0
Vesuvius dock and bay rocks	–	3	–	0	–	0
Six small islets and beacons (solitary nests)	6	6	1	0	0.16	0
Total	**555**	**1322**	**172**	**389**		
Average fledging rate					**0.31**	**0.29**
Chain Islands						
Great Chain Island	–	1876	–	–	–	1.0–1.5 (est.)
Other Chain Islands (12 islets, see inset in Fig. 1)	–	536	–	590	–	1.1

[a] Disturbance by eagles.
[b] Disturbance by otters.

southern portion of the Strait of Georgia. The expanding gull population in the strait is apparently facilitated by an increasing supply of such refuse (Drent and Guiguet 1961; Vermeer 1963; Butler *et al.* 1980).

The total gull population in the colonies—censused by Drent and Guiguet (1961) in 1959 and 1960 and by Campbell (1976) in 1974 and 1975—has since increased further (Table 4). There were about 2000 more nesting pairs in 1975 than in 1960, and a further 2000 more in 1986 than in 1975. Not all colonies have increased in size: some smaller and moderate-sized ones have declined. Except for Ballenas Island, all colonies censused by Drent and Guiguet 26 yr ago are still used by gulls.

As already noted, the total gull population in the Strait of Georgia has increased markedly since 1960. In 1960, there were on average 6150 nesting pairs in the strait (Table 4). Campbell (1976) observed a total of 9791 nests in the strait in 1974 and 1975, and we counted 13 002 nests in 1986. The nesting population appears to have at least doubled from 1960 to 1986, at an average rate of about 2.9% per year. This rate can be further subdivided to indicate an average yearly increase in pairs of about 3.1% between 1960 and 1975, and about 2.6% between 1975 and 1986.

6.2. Mortality and predation

Vermeer (1963) observed that Glaucous-winged Gulls on Mandarte Island produced 1.0 and 1.7 fledglings per nesting pair in 1961 and 1962, respectively. The observed rate of 1.4 fledglings per nest on Mandarte Island in 1985 and 1986 falls well within that range, indicating similar reproductive success on the island in the 1960s and 1980s. Predation may be the primary cause of low reproductive success of solitary pairs and of small to moderate-sized colonies in the Gulf Islands. Northwestern Crows (*Corvus caurinus*) were seen preying upon gull eggs on several islands that we censused. As we approached a nesting island, gulls would leave, and crows would use that opportunity to take the eggs. Northwestern Crows are known to prey extensively upon cormorant and gull eggs under such circumstances (Drent *et al.* 1964; Verbeek 1982) but have infrequently been observed to do so at times without disturbance. Therefore, it is unlikely that crows would cause reproductive failure of a small gull colony, unless chronically disturbed by human visitors or predators. Bald Eagles (*Haliaeetus leucocephalus*) apparently caused chronic disturbance on South Islet (near Mandarte Island) in 1985 and 1986 and on Arbutus, Ragged, and Rose islands in 1986, as eagles were present each time we

Figure 2
Growth of nesting population of Glaucous-winged Gulls on Mandarte and Mitlenatch islands. Population counts or estimates until 1960 are from Drent and Guiguet (1961); in 1962 from Vermeer (1963); in 1975 from Campbell (1976); and in 1985–86 from this study. Curves are estimated by eye.

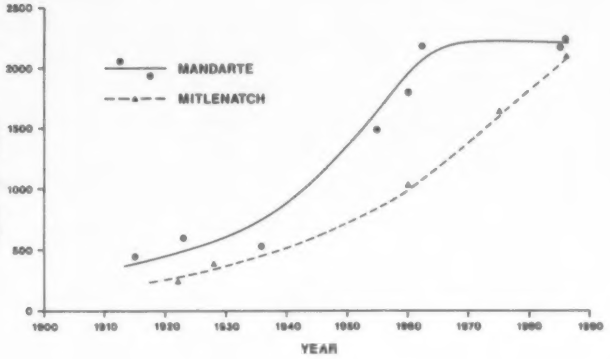


Table 4
Comparison of Glaucous-winged Gull census on islands in the Strait of Georgia in 1959–60 (Drent and Guiguet 1961), 1974–75 (Campbell 1976), and 1986 (this study)

	No. of nests (pairs)		
Name of nesting locality	**1959–60**	**1974–75**	**1986**
Mitlenatch Island	900–1200 (est.)	1632	2 100
St. John Point, Hornby Island	30 (est.)	5	6
Sisters Islets	100 (est.)	108	25
Ballenas Island	50 (est.)	0	0
Franklin and Merry islands	600 (est.)	639	222
White Islets	No estimate	279	490
Christie Islet and Pam Rock	299	598	563
Passage Island and rock to south, Howe Sound	50	496	384
Hudson Rocks and Five Finger Island	80	559	911
Snake Island	300–500 (est.)	558	673
Ballingall Islets	57	96	140
Java Islets	372	372	298
Imrie Island	270	298	216
Mandarte Island	1800–2000 (est.)	1047	2 259
Chain Islands	700–1000 (est.)	1764	2 432
Trial Island	46	1	No count
Total no. of nests (pairs)	**5654–6654**	**8452**	**10 719**

visited, and the gulls were absent from nests where the eagles perched. Gulls on those islands experienced total (or nearly total) reproductive failure (Table 3). Most (or sometimes all) nests on those islands were empty, whereas others had broken eggshells; eggs were also often found to be gathered at what appeared to be storage sites and showed signs of having been pierced by bird beaks. Bald Eagles have been observed to eat Glaucous-winged Gull eggs (C.J. Henny, pers. commun.), and crows are known to take eggs to storage sites (Verbeek 1982).

Eagles have become much bolder during their visits to gull colonies over the last 25 yr. They also visit colonies more frequently. In 1961 and 1962, one or two eagles commonly flew over Mandarte Island and often drove the gulls into the air (KV, pers. obs.). At that time eagles rarely landed on the few trees on the island or on top of the bare cliffs where the cormorants nested. Verbeek (1982) observed similar behaviour during his 1976–80 study, but eagles visited the island much more frequently during 1978–80 than during 1976–77. In 1985 and 1986, we observed four to 12 adult and immature eagles sitting on the ground on South Islet and the adjacent southern tip of Mandarte Island each time we visited. The increased visitation by eagles of gull colonies corresponds to an increase of Bald Eagles in the region. The nesting population of Bald Eagles has increased by at least one-third in the Gulf Islands over the last 10 yr (Vermeer, Morgan, Butler, and Smith, this publication). Adult gull predation by eagles appears extensive. Glaucous-winged Gulls are the most important prey of nesting eagles in the Gulf Islands (Vermeer, Morgan, Butler, and Smith, this publication). Hayward *et al.* (1977) and Verbeek (1982) observed Bald Eagles preying upon adult gulls and chicks in colonies. We observed an eagle fly low over the water towards a gull colony, go over a ridge, and kill an adult gull.

The river otter (*Lutra canadensis*) has recently become a serious predator of Glaucous-winged Gull adults and chicks in the Strait of Georgia (Foottit and Butler 1977; Verbeek and Morgan 1978). River otter predation appears to have caused reproductive failure of gulls on Imrie Island in 1985. Otter scats were observed in trampled paths that led through tall grass from the water to nests on the island. All nests were empty, and several carcasses of adult gulls were found. A few otters as well as many scats were seen at two other nesting localities in the Gulf Islands (Table 3) and in several other colonies in the strait that were not investigated for reproductive success. This suggests that otters visit many colonies.

6.3. Present rate of increase

After the chicks are fledged and leave the colony, mortality continues to be high for first-year birds, probably in part because of their inexperience in finding food (Verbeek 1977*a*, 1977*b*; Searcy 1978). Butler *et al.* (1980) calculated first-year mortality to be 59.2%, based on a life table constructed on 1002 band recoveries of banded chicks. This mortality rate is similar to what has been observed for the closely related and similar-sized Herring Gull (*Larus argentatus*). The Herring Gull in Denmark, Fenno-Scandia, and the United States has a mortality rate during the first year after fledging of 62, 57, and 60%, respectively (Paludan 1951; Hickey 1952; Olsson 1958). After the first year, the mortality figures of these authors disagree. Calculated mortality based on band recoveries is much biased because of band loss in later years (Paynter 1966). Observations of survival of banded gulls are more reliable for determining adult survival. Vermeer (1963) observed that 59 of 68 colour-banded nesting adults returned the year after they were banded on Mandarte Island and estimated an annual survival rate of 90%. Drost *et al.* (1961), who conducted a long-term study of Herring Gulls in Germany, calculated the annual survival of banded adults to be 90%. Coulson and Butterfield (1986) observed an average 91.7% annual survival of 44 to 50 colour-banded nesting Herring Gulls in Britain from 1979 to 1985. Calculated and observed adult survival rates of Herring and Glaucous-winged gulls are therefore similar.

One can calculate the present rate of increase of the Glaucous-winged Gull population in the Strait of Georgia from observed chick and adult survival and estimated post-fledging survival. About half the 13 000 breeding pairs in the strait nest on Chain, Mandarte, and Mitlenatch islands. Those on Chain and Mandarte islands had an average fledging rate of 1.4 fledglings per nest per year. There are no data for Mitlenatch Island. The fledging rate of the other half of the breeding population in the Strait of Georgia may be similar to that observed both for solitary pairs and for small to moderate-sized colonies in the Gulf

Islands, which averaged 0.3 fledglings per nest. The combined fledging rate of all colonies in the strait is estimated to average 0.85 per nest per year. At that rate, 13 000 pairs of gulls in the strait could produce about 11 000 fledglings per year. At an estimated mortality of 59% (Butler *et al.* 1980), about 4500 of these fledglings would survive their first year of life after colony departure.

Although there are no direct observations on the survival rates of juveniles and subadults, it is known that most of this 59% mortality of first-year juveniles occurs during the first seven months after fledging (Verbeek 1986). After seven months, the mortality approaches that of adults. Glaucous-winged Gulls breed for the first time when 4 yr old (Vermeer 1963). Because mortality after the first seven months approaches that of adults, mortality of 2, 3, and 4 yr olds may be similar to that of adults. We estimate, therefore, that about 3300 of the 4500 first-year juveniles will reach the age of first breeding. Annual adult mortality (10%) of 13 000 pairs (= 26 000 gulls) is calculated to be 2600 birds. If our assumptions are correct, the present rate of increase of the gull population in the Strait of Georgia (2.7%) is practically the same as that for the previous 11 yr (2.6%).

6.4. The population at the strait's edge

Around the time that Drent and Guiguet (1961) conducted their survey, there was only one report of a pair of roof-nesting Glaucous-winged Gulls in Vancouver (Oldaker 1963). In 1986, Vermeer *et al.* (1988) estimated that about 500 pairs of Glaucous-winged Gulls nested on buildings along Burrard Inlet and False Creek, Vancouver. Most of the gull increase appeared to have occurred there during the previous 6 yr. Hooper (1987) estimated that about 110 pairs nested on buildings in Victoria in 1986. Many of the gulls on roofs in Vancouver and Victoria nest solitarily or in small groups of two to 10 pairs, but colonies of up to 80 pairs also exist (Vermeer *et al.* 1988). It is not clear whether the expansion of roof-nesting gulls results from "an overflow" of gulls nesting in the Strait of Georgia or from a high recruitment rate of "city gulls" themselves. Initial gull settlement on roofs may have resulted from such an overflow and/or the attraction of safe nesting sites on roofs and nearby food. Once settled, the high reproductive success of solitary nesters and small groups of gulls on roofs could account for much of the present city gull increase (Vermeer *et al.* 1988). Roof-nesting gulls are now rapidly colonizing the urban waterfront along the strait. Studies of roof-nesting gulls in Great Britain indicate that Lesser Black-backed Gulls (*Larus fuscus*) and Herring Gulls are doubling their populations every 3 and 5 yr, respectively (Coulson and Monaghan 1978).

7. Recommendations for further studies

The Glaucous-winged Gull population in the Strait of Georgia, as well as that residing on roofs of buildings on the urban waterfront, should be censused every 10 yr. A census should reveal if the population in the strait continues to increase at the same rate as in previous years, and if that on the urban waterfront continues to expand rapidly. If the population on the urban waterfront continues to increase at the present rate, management of that population will become essential.

Because predation by Bald Eagles and river otters on Glaucous-winged Gulls appears substantial, studies on the interaction between eagles and gulls, and otters and gulls, are desirable.

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Population trends and nesting habitat of Double-crested and Pelagic cormorants in the Strait of Georgia

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1. Abstract

The nesting populations of Double-crested (*Phalacrocorax auritus*) and Pelagic (*P. pelagicus*) cormorants were surveyed in the Strait of Georgia in 1987. The most recent previous survey was conducted in 1983. Populations of Double-crested Cormorants increased between 1983 and 1987 but to a lesser degree than between 1960 and 1983, whereas those of Pelagic Cormorants leveled off.

Observations on nesting habitat showed that Double-crested Cormorants nested primarily on the ground, whereas Pelagic Cormorants nested along cliff faces of islands. Both species nested significantly more on islands with gulls than on those without. At Great Chain Island, where Double-crested and Pelagic cormorants nested near one another on the ground, nearest-neighbour distances between nests were similar for the two species; however, Pelagic Cormorants nested closer to shore, nearer to the water surface, and on narrower nesting ledges than did Double-crested Cormorants. For building nests, Double-crested Cormorants used mainly branches, whereas Pelagic Cormorants used mostly grass.

2. Résumé

Les populations de Cormorans à aigrettes (*Phalacrocorax auritus*) et de Cormorans pélagiques (*P. pelagicus*) ont été recensées en 1987 dans le détroit de Georgia. Le dernier recensement avait été effectué en 1983. Les populations de Cormorans à aigrettes ont augmenté de 19[illegible] 1987, mais pas autant que de 1960 à 1983, tandis qu[illegible]es populations de Cormorans pélagiques ont atteint un plateau.

Les observations sur les habitats de nidification ont montré que les Cormorans à aigrettes nichaient surtout au sol, tandis que les Cormorans pélagiques nichaient du côté des falaises sur les îles. Pour nicher, les deux espèces préféraient de beaucoup les îles où il y avait des goélands et mouettes. Dans l'île Great Chain, où les Cormorans à aigrettes et les Cormorans pélagiques nichaient au sol les uns près des autres, la distance entre un nid et le nid voisin le plus proche était la même dans le cas des deux espèces; toutefois, les Cormorans pélagiques nichaient plus près du rivage et de la surface de l'eau et sur des corniches plus étroites que les Cormorans à aigrettes. Pour construire leur nid, les Cormorans à aigrettes utilisaient surtout des branches, et les Cormorans pélagiques, de l'herbe.

3. Introduction

Nesting populations of Double-crested (*Phalacrocorax auritus*) and Pelagic (*P. pelagicus*) cormorants have been surveyed in the Strait of Georgia by Drent and Guiguet (1961), Campbell (1976), and Vermeer and Rankin (1984). These surveys indicated that the population of Double-crested Cormorants increased from about 203 nests in 1959–60 to 671 nests in 1974–75, and to 1606 nests in 1983. Corresponding increases for Pelagic Cormorants were from 953 to 2149 and 2438 nests, respectively. These results suggest that the number of Double-crested Cormorants continued to increase from the 1960s to 1983, whereas that of Pelagic Cormorants leveled off. In 1987, we conducted another survey of the nesting populations of those two species in the Strait of Georgia to continue the assessment of population trends. We also collected information on nesting habitat and nest sites of the two species.

4. Methods

The surveys were conducted between 5 and 23 June except at Race Rocks, which were investigated on 15 July; a small motorboat was used. Surveys were conducted from the water except on Great Chain Island, Five Finger Island, and Hudson Rocks; at these sites, cormorants were counted on land. Colonies were surveyed one to three times; nest counts took from 5 min to 1 h, depending on the size of the colony.

We also obtained information on the nesting habitat of each colony in the Gulf Islands. We circled all islands ($n = 284$) by boat and noted the extent of forestation ($>50\%$ = forested) and whether islands were inhabited by people or nesting Glaucous-winged Gulls (*Larus glaucescens*).

Where the two species nested close to one another on Great Chain Island, we measured the distance of nests from shore, their height above the water surface (high tide), the distance to the nearest conspecific nest, the maximum width of the nest ledge, the nest diameter and height, and the percent composition of nest material. Thirty Double-crested and 30 Pelagic cormorant nests were involved in these measurements.

The statistical analyses done in this paper relate mainly to comparisons of nesting with nonnesting islands (see Table 4), and of nest characteristics of Double-crested Cormorants with those of Pelagic Cormorants on Great Chain Island (see Table 5). The distribution of the data that are summarized in these tables is highly skewed, with variances that are not homogeneous. Hence, comparisons of means cannot be carried out using classical two-sample t-tests, F-tests, or even some nonparametric tests. Hence, inferences about equality of the medians and the distributions were made by use of two-way chi-square contingency tables. However, the means and standard deviations are presented strictly for descriptive purposes.

For each variable in each table, the islands (or nest sites) were divided into two or three categories with approximately the same number of islands (or nest sites) in each. A two-way contingency table was then constructed to test for significant differences.

5. Results and discussion

5.1. Populations

5.1.1. *Overall rates of increase*

Double-crested Cormorants were observed in 11 colonies (Fig. 1), and Pelagic Cormorants in 26 colonies (Fig. 2), in the Strait of Georgia in 1987. For these two species, the survey results for 1987 are compared with those for 1959–60, 1974–75, and 1983 in Tables 1 and 2. The overall population of Double-crested Cormorants appeared to be still increasing as of 1983. The average rate of annual increase for this species was 8.3, 11.5, and 5.4% between 1960 and 1975, 1975 and 1983, and 1983 and 1987, respectively. However, the 1983–87 rate of increase for Double-crested Cormorants was much less than in preceding time periods. Corresponding average rates of annual change for Pelagic Cormorants over the same periods were 5.6, 1.6, and −1.0%, respectively, which indicates that the population of Pelagic Cormorants increased little since 1975.

5.1.2. *Population growth*

Five new colonies each of Double-crested and Pelagic cormorants were observed in 1987 (Tables 1 and 2). The Double-crested Cormorant colony that currently has the fastest rate of growth is on the Chain Islands (Table 2). Mandarte Island continues to have the largest colonies of Double-crested and Pelagic cormorants in the Strait of Georgia, but those populations have not increased over the last 4 yr (Tables 1 and 2). The Double-crested Cormorants began nesting in the Strait of Georgia in the late 1920s, and the first colony to be discovered was that on Mandarte Island (Munro 1928; Drent and Guiguet 1961). It is interesting to compare the growth of the Double-crested Cormorant colony on Mandarte Island with that of the Pelagic Cormorant, which was probably established there between 1910 and 1915 (Fig. 3). The populations of both species may be leveling off at present, but surveys are needed in the near future to confirm this.

5.1.3. *Population decreases*

Bare Point, which had the second largest colonies of Double-crested and Pelagic cormorants in 1983, has since been abandoned by Double-crested Cormorants, whereas by 1987 the population of Pelagic Cormorants had been reduced to 38% of the 1983 value. Bare Point is part of Vancouver Island and has recently been the scene of much logging activity; Double-crested Cormorants may have abandoned the locality as a result of that activity. One new Double-crested Cormorant colony on dolphins near Crofton and one new Pelagic Cormorant colony on Tent Island, 6.5 and 5.7 km, respectively, from Bare Point, have become established since 1983. Perhaps the cormorants moved from Bare Point to the new localities as a result of disturbance. Double-crested Cormorants on Franklin Rock, Merry Island, and Rose Islets were further reduced in number between 1983 and 1987 (Table 1). The colony on Rose Islets decreased in 1983 as a result of disturbance by pleasure boaters (Vermeer and Rankin 1984); perhaps this has continued there since 1983. Several colonies of Pelagic Cormorants, such as those on Passage Island, Five Finger Island, and East Point on Saturna Island, have notably decreased since 1983 for unknown reasons. Those at Five Finger Island and Hudson Rocks are situated so close to one another (Fig. 1) that a disturbance at one colony could easily result in an increase of cormorants at the other.

5.2. Nesting habitat

5.2.1. *Habitat plasticity*

Both Double-crested and Pelagic cormorants showed much plasticity in nesting habitat (Table 3). Most Double-crested Cormorant colonies, however, were established on the ground, and most Pelagic Cormorant colonies were found on cliffs on islands (Table 3). In 1987, only one Double-crested Cormorant colony, that on Ballingall Islets, occurred in trees. In 1983, the colony on Bare Point was also situated in trees. One Pelagic Cormorant colony was observed by Hobson and Wilson (1985) to be located on the support beams of the spans of the Second Narrows Bridge, a cantilever-type highway bridge spanning Burrard Inlet. About 10 nests were observed at that locality in 1983, and 63 in 1984. In 1985, 85 nests were removed by the Ministry of Transport and Highways. No nests were removed in 1986 and 1987, and 90 nests with eggs and young were observed on the bridge by D. Wilson (pers. commun.) in 1987. In neighbouring Washington State, Pelagic Cormorants established a colony on a wooden tower at Port Townsend (Wahl and Speich 1984), on pilings at Port Angeles, and on a decaying pier in Dungeness (T.R. Wahl, in Hobson and Wilson 1985). On the west coast of Vancouver Island, Carter *et al.* (1984) found small colonies of Pelagic Cormorants on ledges in caves, as well as on arches. We observed several Pelagic Cormorants nesting in cavities on cliffs in the Gulf Islands.

5.2.2. *Tree nesting*

The number of tree-nesting colonies of Double-crested Cormorants across Canada has been found to vary from 9% in the Strait of Georgia (Table 3) to 12.6% ($n = 56$) in the Canadian Prairie provinces (Vermeer 1973), and to a majority ($n = 30$) in Nova Scotia (Lock and Ross 1973). The difference in the number of tree-nesting colonies between British Columbia and Nova Scotia does not appear to relate to nest site competition between related species. Double-crested Cormorants readily nest on the ground on islands with Pelagic Cormorants in British Columbia (this study) and Great Cormorants (*Phalacrocorax carbo*) in Nova Scotia (Lock and Ross 1973). Different forms and degrees of disturbance by people and various predator species may determine whether Double-crested Cormorants nest in trees. Lewis (1929) reported that Double-crested Cormorants started to nest in trees after their former ground-nesting habitat was disturbed by people.

5.2.3. *Presence of gulls*

In the Gulf Islands, there were no significant differences between nesting and nonnesting islands with respect

Figure 1
Distribution of nesting sites of Double-crested Cormorants in the Strait of Georgia in 1987. Numbered colonies are identified in Table 1.

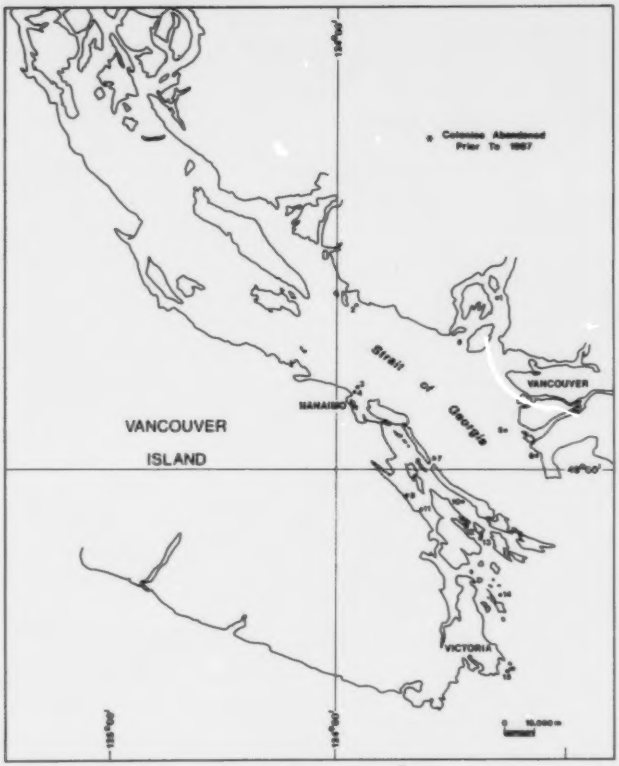
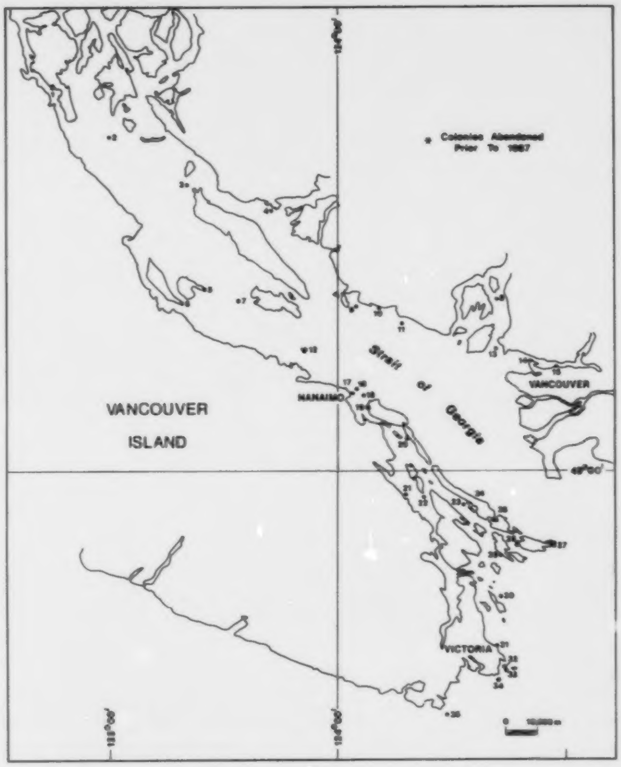


Figure 2
Distribution of nesting sites of Pelagic Cormorants in the Strait of Georgia in 1987. Numbered colonies are identified in Table 2.



to forestation and human inhabitation, but both cormorant species nested significantly more on islands where nesting gulls were present (Table 4). The presence of gulls may indicate to cormorants a site relatively safe from mammalian predators.

5.3. Nest sites

Both cormorant species nested close to one another on the ground on Great Chain Island. The terrain did not restrict Pelagic Cormorants from nesting close to one another, which could have been the case if the cormorants nested on cliff ledges. When Pelagic Cormorants nested on cliffs, they often nested close to one another in pockets where there was sufficient room on ledges; however, many Pelagic Cormorants also nested on small isolated ledges. On Great Chain Island, Pelagic Cormorants nested on significantly narrower ledges, closer to shore, and lower above the water surface than did Double-crested Cormorants (Table 5). We also observed that, when the two species nested together on other islands in the Strait of Georgia, Pelagic Cormorants generally occupied the narrow ledges on cliff faces, whereas Double-crested Cormorants nested on the tops of cliffs. Also, Pelagic Cormorants nested seaward of Double-crested Cormorants on islands other than Great Chain Island.

We observed that the nearest-neighbour distances between nests of the two cormorant species on Great Chain Island were similar (Table 5). However, Siegel-Causey and Hunt (1981), who studied the colonial defense behaviour of the two species on Mandarte Island, observed that the average nearest-neighbour distances for nests was 1.2 m for Double-crested Cormorants and about 1.7 m for Pelagic Cormorants. This difference was considered by them to be highly significant. They also observed that Pelagic Cormorants had more isolated nests than Double-crested Cormorants. They used these criteria to support the hypothesis that species whose colonies are accessible to predators should form tighter groupings than species with reduced accessibility to predators. We can foresee, however, situations where Pelagic Cormorants nest as densely as Double-crested Cormorants on cliff ledge pockets, and where Pelagic Cormorants would be comparatively less accessible to predators than Double-crested Cormorants. Because the distribution of isolated Pelagic Cormorant nests on cliffs appears to be brought about chiefly by restriction of terrain (also pointed out by Siegel-Causey and Hunt 1981), one would not need to invoke predation pressure as being responsible for the difference in nest distribution between the two species.

The chief nest material used by each of the two species on Great Chain Island was significantly different. Double-crested Cormorants used mostly wooden branches, whereas Pelagic Cormorants used mostly grass (Table 5). This difference in nest composition between the two cormorant species was also observed at other nesting localities in the Strait of Georgia, although the composition of nest material in these cases was not quantified. The reason that Double-crested Cormorants use mostly tree branches and Pelagic Cormorants rarely do is unknown. Because Double-crested Cormorants also nest in trees and Pelagic Cormorants do not, the former species may be more familiar with tree habitat than is the latter. This could explain

Table 1
Comparison of number of nests in Double-crested Cormorant colonies in the Strait of Georgia: 1959–60 (Drent and Guiguet 1961); 1974–75 (Campbell 1976); 1983 (Vermeer and Rankin 1984); and 1987 (this study)

Colony location[a]	1959–60	1974–75	1983	1987
1. Christie Inlet and Pam Rock	–[b]	29	120	119
2. Franklin Rock and Merry Island	–	54	21	5
3. Five Finger Island	–	–	–	138
4. Hudson Rocks	–	–	–	17
5. Sand Heads (8 dolphins)	–	–	–	86
6. Westshore Terminal Range Lights	–	–	–	42
7. Canoe Islet	–	12	–	–
8. Rose Islets	–	80	12	2
9. Bare Point (Chemainus)	–	–	198	–
10. Ballingal Islets	28	14	20	25
11. Shoal Islands (2 dolphins)	–	–	–	65
12. Second Sister Island (Chain Islands)	9	–	–	–
13. Channel Islands	16	–	–	–
14. Mandarte Island	150	482	1100	972
15. Chain Islets	–	–	135	510
Total no. of nests observed	203	671	1606	1981

[a] Locations of numbered colonies are shown in Figure 1.
[b] Nests present in 1941 but not counted.

Table 2
Comparison of number of nests in Pelagic Cormorant colonies in [illegible] of Georgia: 1959–60 (Drent and Guiget 1961); 1974–75 (Campbell [illegible] 1983 (Vermeer and Rankin 1984); and 1987 (this study)

Colony location[a]	1959–60	1974–75	1983	1987
1. Quadra Island	Nesting in large numbers	–	–	–
2. Mitlenatch Island	155	286	318	315
3. Vivian Island and Rebecca Rock	–	25	15	3
4. McRae Islet	–	–	–	15
5. St. John Point, Hornby Island	50[b]	9	127	101
6. Chrome Island	–	54	78	141
7. Sister Islets	–	41	51	–
8. Christie Islets and Pam Rock	Colony declining—a few unsuccessful nests	3	80	44
9. Franklin Rock and Merry Island	–	130	18	22
10. Trail Islands	–	2	15	14
11. White Islets	–	4	38	13
12. Ballenas Islands	Undetermined no. of nests	24	–	–
13. Passage Island	–	48	72	16
14. Prospect Point and Siwash Rock	–	–	64	93
15. Second Narrows Bridge	–	–	10	90
16. Five Finger Island	–	} 91	115	17
17. Hudson Rocks	38		30	142
18. Snake Island	15	22	60	74
19. Gabriola Island cliffs	7	367	–	–
20. Valdes Island cliffs	6[b]	–	6	–
21. Bare Point (Chemainus)	50	118	373	142
22. Tent Island cliffs	–	–	–	74
23. Ballingal Islets	11	–	–	2
24. Galiano Island cliffs	–	–	–	72
25. Active Pass	–	1	–	–
26. Elliot Bluff, Saturna Island	–	10	–	–
27. East Point, Saturna Island	–	54	53	12
28. North Pender Island cliffs	–	–	–	8
29. Arbutus Island	–	–	16	18
30. Mandarte Island	375	443	550	536
31. Gordon Head cliffs	20[b]	20	13	24
32. Harris Island and Lewis Reef	–	54	–	–
33. Chain Islands	74	183	203	248
34. Trial Island	107	–	–	–
35. Race Rocks	45	160	143	120
Total no. of nests observed	953 (minimum)	2149	2448	2356

[a] Locations of numbered colonies are shown in Figure 2.
[b] Counts in 1955–56.

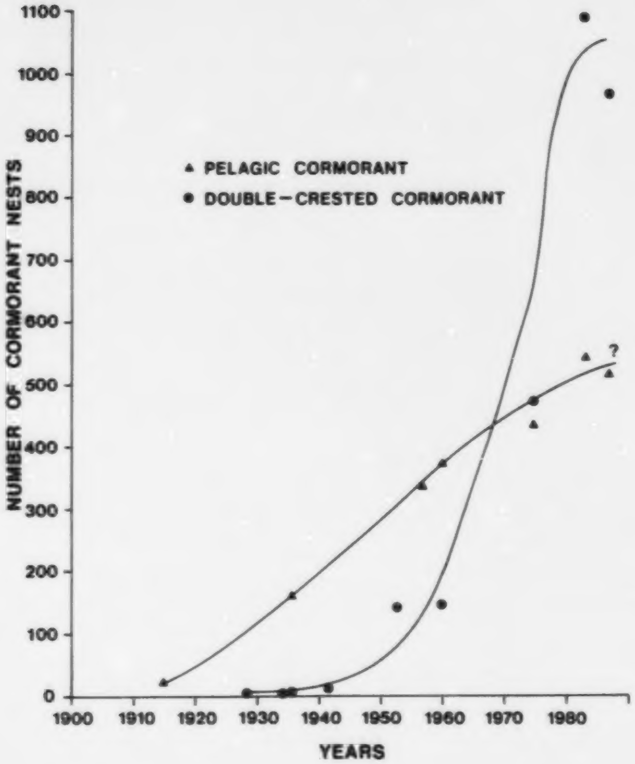
the large proportion of branches in Double-crested Cormorant nests.

6. Recommendations for further studies

(1) Surveys should be conducted in the future to determine if the number of Double-crested Cormorants in the Strait of Georgia is increasing or leveling off.

(2) Cormorants at several colonies should be banded. Without a study of marked birds, there can be no proof that new colonies result from abandonment of old ones.
(3) A population study of the two cormorant species should be conducted to understand population fluctuations. Little is known about survival rates of adult and immature cormorants; data on reproductive success of cor-

Figure 3
Comparison of number of breeding pairs or nests of Double-crested and Pelagic cormorants observed on Mandarte Island, 1915–87 (Drent *et al.* 1964; this study). Curves are estimated by eye only.



morants exist only for Mandarte Island (Drent *et al.* 1964; Robertson 1971). Vermeer and Devito (this publication) show that reproductive success of Glaucous-winged Gulls (*Larus glaucescens*) varies considerably from one colony to the next.

7. Acknowledgements

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Table 3
Comparison of locations of nesting colonies of Double-crested and Pelagic cormorants in the Strait of Georgia, 1987

	Double-crested Cormorant		Pelagic Cormorant	
Locations	**No. of sites (%)**	**No. of nests (%)**	**No. of sites (%)**	**No. of nests (%)**
Ground[a]	7 (63.6)	1763 (89.0)	5 (19.2)	483 (20.5)
Cliff faces	–	–	20 (76.9)	1783 (75.7)
Dolphins, lights	3 (27.3)	193 (9.7)	–	–
Trees	1 (9.1)	25 (1.3)	–	–
Bridge supports	–	–	1 (3.8)	90 (3.8)
Total	**11** (100)	**1981** (100)	**26** (100)	**2356** (100)

[a] "Ground" on an island is defined here as any place relatively level compared with a cliff face.

Table 4
Proportions (%) of variables for islands with and without nesting cormorants in the Gulf Islands, 1987

			Significance		
Island characteristics	**Nesting islands**[a]	**Nonnesting islands**[b]	χ^2	**df**	***P***
Double-crested Cormorant					
% forested	0.0	40.6	2.63	1	0.10
% inhabited by people	16.7	25.9	0.002	1	0.97
% where nesting gulls present	100.0	20.5	17.14	1	0.000
Pelagic Cormorant					
% forested	36.4	39.9	0.0008	1	0.98
% inhabited by people	35.4	25.3	0.22	1	0.64
% where nesting gulls present	90.9	19.4	27.31	1	0.000

[a] For Double-crested Cormorant, n = 6; for Pelagic Cormorant, n = 11.
[b] For Double-crested Cormorant, n = 278; for Pelagic Cormorant, n = 273.

Table 5
Comparison of nest parameters for 30 Double-crested and 30 Pelagic cormorant nests located on the ground on Great Chain Island in 1987

	Double-crested Cormorant		Pelagic Cormorant		Significance		
Nest parameters	**Mean ± SD**	**Median**	**Mean ± SD**	**Median**	χ^2	**df**	***P***
Nest site (measurements in metres)							
Distance to nearest conspecific nest (pecking distance, outer rim to outer rim)	0.45 ± 0.07	0.45	0.53 ± 0.26	0.45	0.00	1	1.00
Minimum distance to shore	23.6 ± 1.4	23.2	15.3 ± 5.2	12.1	27.1	1	0.000
Height above water surface	8.1 ± 0.4	8.1	4.9 ± 1.6	4.4	36.7	1	0.000
Maximum width of nesting ledge	2.1 ± 1.0	2.1	0.53 ± 0.23	0.48	42.0	1	0.000
Nest diameter (outside)	0.54 ± 0.06	0.55	0.44 ± 0.04	0.44	32.3	1	0.000
Nest height	0.25 ± 0.11	0.22	0.26 ± 0.09	0.25	0.75	1	0.69
Composition of nest material (%)							
Branches	65.0 ± 14.8	70	1.7 ± 2.6	1	52.3	1	0.000
Kelp, eelgrass	13.3 ± 9.1	11	20.0 ± 11.6	20.5	11.7	1	0.003
Grass	17.8 ± 7.0	15.5	75.1 ± 13.7	76.5	52.3	1	0.000
Miscellaneous materials[a]	3.9		3.2				

[a] Include gull feathers, cedar bark, rock, and man-made objects.

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The breeding biology and distribution of the Pigeon Guillemot (*Cepphus columba*) in the Strait of Georgia

Simon K. Emms and Ken H. Morgan

1. Abstract

The breeding biology of the Pigeon Guillemot (*Cepphus columba*) in the Strait of Georgia is described, based mainly on the studies of Drent (1965), Koelink (1972), and Emms (1987, and unpubl. data). Breeding chronology is similar to that of other populations of *Cepphus* guillemots. Reproductive success is much higher on Mandarte Island than on Mitlenatch Island, owing largely to intense snake predation on young chicks on Mitlenatch Island. Mean clutch size and the proportion of suitable nest holes occupied are also higher on Mandarte Island, although the relationships between these factors are unclear. Long-term demographic studies will be needed if we are to add to our knowledge of the species and to understand the factors influencing its life history strategy.

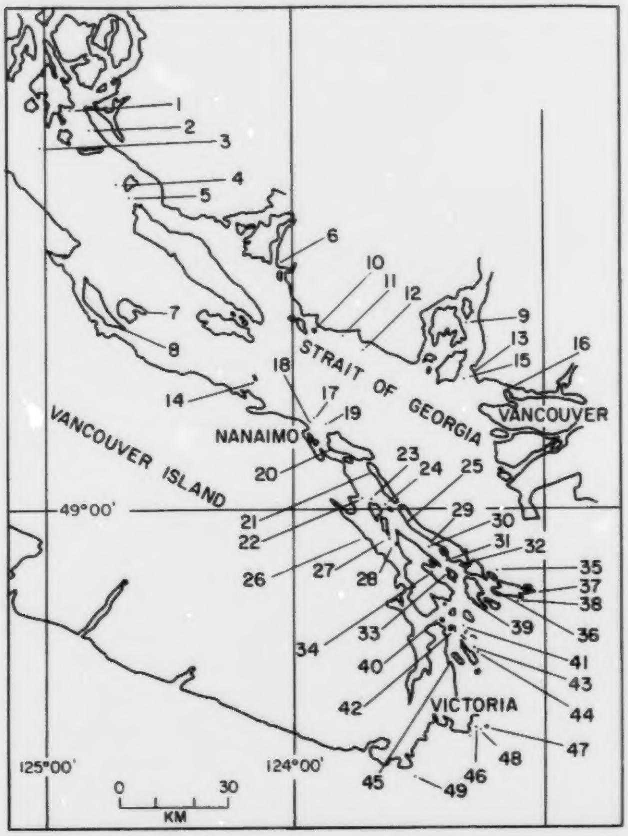
2. Résumé

Les auteurs décrivent les caractéristiques de la reproduction du Guillemot du Pacifique (*Cepphus columba*) dans le détroit de Georgia en se fondant surtout sur les études de Drent (1965), de Koelink (1972) et d'Emms (1987, données non publiées). La chronologie de la reproduction est la même que pour d'autres populations de Guillemots du Pacifique. Le succès de la reproduction est beaucoup plus élevé dans l'île Mandarte que dans l'île Mitlenatch surtout parce que, à ce dernier endroit, les serpents mangent beaucoup d'oisillons. En outre, dans l'île Mandarte, le nombre moyen d'oeufs par couvée est plus elevé, et la proportion de terriers convenables pour la nidification qui sont occupés est plus grande, bien qu'un rapport entre ces facteurs n'ait pas été clairement établi. Il faudra effectuer des études démographiques à long terme pour en connaître davantage au sujet de cette espèce et comprendre les facteurs qui influent sur sa façon de vivre.

3. Introduction

The Pigeon Guillemot (*Cepphus columba*) is a medium-sized (400 g) alcid that breeds on the coasts of the northern Pacific Ocean. In North America, it ranges from northern Alaska, the Bering Sea, and the Aleutian Islands to southern California; in Asia, it ranges from the Chukotski Peninsula to the Kurile Islands (American Ornithologists' Union 1983). It breeds along all of the BC coast and occurs in relatively small numbers throughout the Strait of Georgia (Fig. 1).

Figure 1
Breeding sites of Pigeon Guillemots in the Strait of Georgia. Information was compiled from Drent and Guiguet (1961), Campbell (1976), and KM's 1987 survey. See Table 1 for estimates of breeding populations at each site.



The breeding biology of the species has been investigated by Storer (1952), Thoresen and Booth (1958), and Kuletz (1983) and in three studies conducted in the Strait of Georgia (Drent 1965; Koelink 1972; Emms 1987). Drent's (1965) study was carried out on Mandarte Island in 1959 and 1960, building on preliminary work by G.F. van Tets in 1957 and 1958. Mandarte Island (48°38′N, 123°17′W) is a small island, 700 m long and 100 m broad, lying among the Gulf Islands of Haro Strait. It holds the second largest breeding population of Pigeon Guillemots in the Strait of Georgia, estimated by Drent (1965) to be 100 to 110 pairs. Drent's (1965) work covered all aspects of the species' breeding biology but placed special emphasis on detailed descriptions of behaviour patterns (see also Nelson 1984) and on the development of thermoregulation by the chicks. Koelink (1972), also working on Mandarte Island, concentrated on the bioenergetics of chick rearing and further developed Drent's (1965) studies on thermoregulation. Emms (1987) worked on Mitlenatch Island and concentrated on factors influencing the pattern of nesting dispersion. Mitlenatch Island (49°57′N, 125°00′W), lying 300 km to the northwest of Mandarte Island, is a much larger island and holds the largest breeding population of guillemots in the Strait of Georgia—approximately 175 to 200 pairs (Drent and Guiguet 1961; SKE, unpubl. data).

4. Breeding distribution

The breeding distribution of the Pigeon Guillemot in the Strait of Georgia was surveyed (by KM) in 1987. All islands, islets, and rocks from Five Finger Island south were surveyed between 5 and 23 June. North of Five Finger Island, only previously known colonies and cormorant colonies were surveyed on 8 and 9 July. Race Rocks was surveyed on 15 July. All birds seen flying to or from potential nest sites, sitting on rocks near potential nest sites, or within 50 m offshore of these sites were counted. For most of the larger colonies, either several passes were made around the island or the island was revisited at a later date. In all such cases, the highest count is given here. The data are summarized in Table 1 and Figure 1, along with information from Drent and Guiguet (1961) and Campbell (1976). Unfortunately, it is difficult to compare these data sets directly, because the data presented are different in each case and because the number of birds present on the nesting grounds is strongly influenced by the time of day (see Section 5). Ewins (1985), studying Black Guillemots, suggested that the best estimates of adult populations are provided by counts made between 05:00 and 08:00, in winds of force 4 or less, during the prebreeding period. Such a procedure should be adopted in future if accurate surveys, comparable with one another, are to be done. However, the data do show that Pigeon Guillemots are distributed throughout the Strait of Georgia, that most breeding sites have only a small number of breeding pairs, and that two major colonies—Mandarte and Mitlenatch islands—hold nearly half the total breeding population of the strait. It is not possible to tell whether there has been a significant change in the breeding population since Drent and Guiguet's (1961) survey.

5. Breeding chronology

5.1. The prelaying period

Pigeon Guillemots begin to return to their breeding grounds in the Strait of Georgia in early spring, and by late April moderate numbers of birds can be seen around both Mandarte and Mitlenatch islands. At this time of year, most birds are present only in the early morning hours, arriving at first light and leaving before 10:00–11:00 (Drent 1965; SKE, unpubl. data). At first they simply congregate offshore, where they display to each other in small groups and occasionally engage in "mass flights" of large numbers of individuals, a phenomenon also described for the Black Guillemot (Cairns 1978). The first landings on shore occur during the last week of April (Drent 1965; SKE, unpubl. data), and nest prospecting and reoccupation begin in the first week of May, by which stage many of the birds are obviously paired. Not all the birds are breeders, however. Drent (1965) estimated that 30% of the individuals counted in one section of the Mandarte colony in 1959 were nonbreeders. A similar percentage was found on Mitlenatch Island in 1984. Drent (1965) found that the nonbreeders on Mandarte Island consisted of small numbers of 1 yr olds and larger numbers of 2 yr olds. The age at first breeding and the proportion of nonbreeders among older birds are not known. Petersen (1981) summarized available data on the Black Guillemot and suggested that breeding first occurs at 4 yr, sometimes 3, and perhaps occasionally 2.

Pigeon Guillemots are hole nesters and are extremely flexible in their choice of nest site (Storer 1952). On both Mandarte (Drent *et al.* 1964) and Mitlenatch (SKE, unpubl. data) islands, the vast majority of nests are found in chambers in boulder piles on the upper shore, under single boulders on grassy cliff slopes, or in crevices in rock faces. Active excavation of burrows occurs in some areas of the Pacific Northwest (Guiguet 1953; Thoresen and Booth 1958; Drent and Guiguet 1961), and birds will occasionally occupy man-made sites such as harbour pilings (Campbell 1977), as was found on James Island in the 1987 survey.

Unlike the dense colonies formed by most other alcids (Birkhead 1985), guillemots nest mainly in small, loose aggregations. Emms (1987) found that although nests on Mitlenatch Island were highly clumped, this was caused by a clumped distribution of suitable sites. Nests were randomly distributed with respect to the distribution of suitable sites, suggesting that birds were not actively choosing to nest colonially. Only about 50% of suitable holes on Mitlenatch Island were occupied in any one year (Emms 1987); on Mandarte Island, almost all suitable holes were occupied.

Like many other long-lived seabirds (Fisher and Lockley 1954; Lack 1968; Rowley 1983), Pigeon Guillemots are faithful both to previous nest sites and to mates. Drent (1965) recorded four cases of mate retention across 2 or more years and only one case of "divorce." He also found 19 cases of nest site retention across 2 or more years and only six cases of nest desertion. Of these six cases, five occurred after the previous nest site became unusable, and in four cases pairs moved to the nearest available nest hole.

Once a nest site has been occupied, it is defended by both members of the pair against potential intruders. Pairs also defend so-called "beach territories"—small areas on the lower shore where they copulate and spend much of their unoccupied time together. These sites also seem to be retained across seasons, even if nest sites change (Drent 1965). Birds seldom spend time on land away from their own beach sites; those that do wander seem to be males in search of matings, so that defense of these sites may be a means of preventing extrapair copulation.

5.2. The egg stage

In the Strait of Georgia, guillemots lay their eggs from late May to late June. Mean clutch commencement dates range between 2 and 15 June on Mandarte Island and 5 and 11 June on Mitlenatch Island. Nesting appears to be slightly more synchronous on Mitlenatch Island (Table 2). Drent (1965) found a strong correlation between laying dates in successive years for individual

Table 1
Locations of breeding sites of the Pigeon Guillemot in the Strait of Georgia

Location[a]	No. of nests (Drent and Guiguet 1961)[b]	No. of pairs (Campbell 1976)	No. of birds (KM 1987)[c]
1. Three Islets	–	2	4
2. Major Islet	–	2	9
3. Mitlenatch Island	175	200	134
4. Vivian Island	–	35	48
5. Rebecca Rock	–	1	–
6. Daniel Point	20	20	–
7. St. John's Point	10	25	2
8. Chrome Island	–	2	–
9. Christie Islets and Pam Rock	65	17	23
10. Merry Island	–	20	3
11. Trail Islands	–	–	11
12. White Islets	–	8	11
13. Batchelor Point	Adults noted	2	–
14. Ballenas Islands	10	4	4
15. Passage Island	6	20	8
16. Prospect Point and Siwash Rock	1	3	4
17. Five Finger Island	–	15	19
18. Hudson Rocks	–	–	2
19. Snake Island	1	10	6
20. Gabriola Island cliffs	–	2	3
21. Valdes Island cliffs	50	1	–
22. Miami Islet	–	3	–
23. Ragged Islets	–	12	2
24. Rose Islets	–	1	–
25. Galiano Island cliffs (NW of Retreat Cove)	100	–	26
26. Bare Point	–	2	6
27. Tent Island	–	5	2
28. Idol Island	–	2	–
29. Galiano Island cliffs (opposite Ballingall Islets)	–	–	27
30. Ballingall Islets	6	12	13
31. Galiano Island cliffs (Phillimore Point)	–	10	10
32. Active Pass	–	5	15
33. Prevost Island cliffs	–	22	2
34. Third Sister Island (Chain Islands)	–	–	4
35. Belle Chain Islands	–	10	–
36. Elliot Bluff, Saturna Island	30	–	–
37. East Point, Saturna Island	–	–	7
38. Java Islets	8	–	15
39. Oaks Bluff, N. Pender Island	–	–	57
40. Arbutus Island	–	–	28
41. Imrie Island	8	2	8
42. Little Group Islands	–	–	4
43. Mandarte Island	102	100	241
44. Halibut Island	–	–	4
45. James Island dolphins	–	–	8
46. Harris Island	–	–	9
47. Discovery Island	1	–	–
48. Chain Islands	45	30	74
49. Race Rocks	20	80	78
Total	**658 nests**	**685 pairs**	**931 birds**
No. of locations	**19**	**34**	**39**

[a] See Figure 1 for locations.
[b] Data taken from Drent and Guiguet (1961) are the most recent estimates or counts.
[c] When more than one count was made by KM, the highest count is given.

Table 2
Breeding chronology of the Pigeon Guillemot in the Strait of Georgia

		Egg laying date				Clutch size		Incubation period (d)				Fledging period (d)			
Location	Year	$\bar{x}$ (June)	SD	Range	*n*	% one-egg clutches	*n*	$\bar{x}$	SD	Range	*n*	$\bar{x}$	SD	Range	*n*
Mandarte[a]	1957	2.4	5.3	26/5–13/6	19										
	1958	8.2	9.7	18/5–29/6	28										
	1959	14.5	8.0	24/5–28/6	36										
	1960	13.6	7.1	18/5–28/6	41										
	All years	11.0	7.8	18/5–29/6	124	9.3	162	31.2	–	31–34	21	35	–	29–39	15
Mitlenatch[b]	1984	5.0	5.8	26/5–22/6	54										
	1985	7.0	3.5	28/5–16/6	86	22.1	95	31.2	2.83	27–38	41	34.5	2.15	29–37	17
	1986	11.0	5.6	1/6–23/6	74	32.0	78	31.8	3.08	26–40	31				
	All years	8.0	5.4	26/5–23/6	214	26.6	173	31.5	2.94	26–40	72	34.5	2.15	29–37	17

[a] Data for Mandarte Island from Drent *et al.* (1964) and Drent (1965).
[b] Data for Mitlenatch Island from Emms (unpubl. data).

females, suggesting that each bird has a characteristic laying date or laying rank.

Guillemots are unusual among the alcids in laying typically two eggs instead of one. On Mandarte Island, 90.7% of clutches consisted of two eggs and 9.3% of one ($n = 162$). On Mitlenatch Island, proportionately more one-egg clutches were laid: 22.1% in 1985 ($n = 95$) and 32% in 1986 ($n = 78$), figures that are closer to the 21.4% ($n = 42$) found by Thoresen and Booth (1958) in a study in Washington State.

The proportion of one-egg clutches increased as the season progressed in 1984, 1985, and 1986 on Mitlenatch Island, although the effect was significant only in 1984 and 1986 (Table 3). The same effect has been found in Black Guillemots (Preston 1968; Petersen 1981), and it may be simply a consequence of the fact that young birds tend to lay later in the season and produce smaller clutches (Asbirk 1979). However, distinguishing cause from effect is a problem here. It is not known whether earlier breeding and laying larger clutches are both direct consequences of increasing age or whether birds are adjusting clutch size in relation to date independently of age.

There is typically a 3-d interval between laying of the first and second eggs in two-egg clutches (Mandarte: 74% of clutches, $n = 31$ [Drent 1965]; Mitlenatch: 72% of clutches, $n = 72$ [SKE, unpubl. data]), and regular incubation does not begin until the second egg is laid. Drent (1965) used thermistor thermometers taped to eggs in the nest chamber to show that the first egg is incubated intermittently, during the daytime only, before this time. Steady daytime incubation begins on the day following the laying of the second egg, but nighttime incubation may be delayed by up to 3 d. It is possible that the immediate onset of daytime incubation is a means of reducing the risk of egg loss to daytime predators such as Northwestern Crows (*Corvus caurinus*), because almost all egg losses occur during the first few days after laying, when the eggs are not continuously covered by the parents (Drent *et al.* 1964).

If first clutches are lost, birds will sometimes re-lay, replacement clutches appearing after approximately 13 d. However, if one egg of a two-egg clutch is lost, it is not replaced (Drent *et al.* 1964).

5.3. The chick stage

The incubation period averages 31–32 d for the first egg (Table 2). The second egg typically hatches on either the same day as the first or on the next day. Chicks are semiprecocial (Sealy 1973).

The fledging period for the first chick is approximately 35 d (Table 2). In two-chick nests, the chicks sometimes fledge on the same day, but often the second chick fledges 1 or more days after the first; Emms (unpubl. data) recorded intervals of up to 6 d. Birds fledge at close to adult weight: Drent (1965) recorded a mean fledging weight of 411 g ($n = 20$) compared with 450 g ($n = 53$) for adults. Fledging weight was not influenced by hatching date on Mitlenatch Island, although sample sizes were not large (Fig. 2). Fledging occurs at night, and the young become independent of their parents as soon as they fledge. Rarely, parents have been seen to tempt their chicks out of the nest hole with a fish (Winn 1950; Thoresen and Booth 1958). This was observed once during the daytime on Mitlenatch Island, but the chick did not actually fledge at this time (SKE, unpubl. data). On Mitlenatch Island in 1985, when nests were visited daily, the earliest fledging date was 4 August, and five nests still contained chicks when the study ended on 18 August. In 1984, when nests were visited only every 3–5 d, the earliest chicks fledged in the last few days of July, and chicks were still present in nests on 25 August.

6. Reproductive success

6.1. Egg and chick survival

The most striking difference between the guillemot populations on Mandarte and Mitlenatch islands is the much lower reproductive success on Mitlenatch Island (Table 4). This seems to be caused by both a lower hatching success and a much lower fledging success. The reason for the difference in hatching success is unclear. Hatching success on Mitlenatch Island was much lower in 1985, when nests were visited daily, than in 1984, when visits were made every 3–5 d. This decrease was due to both a higher rate of egg predation (10% vs. 24%) and a much higher frequency of abandonment (7% vs. 24%). Drent *et al.* (1964) did not include abandonment as a reason for nest failure, but this could be the cause of the high degree of "addling" they recorded. (If addling and abandonment are grouped together for pooled 1984 and 1985 data on Mitlenatch Island, egg losses due to these causes—23%—are comparable with those on Mandarte Island.)

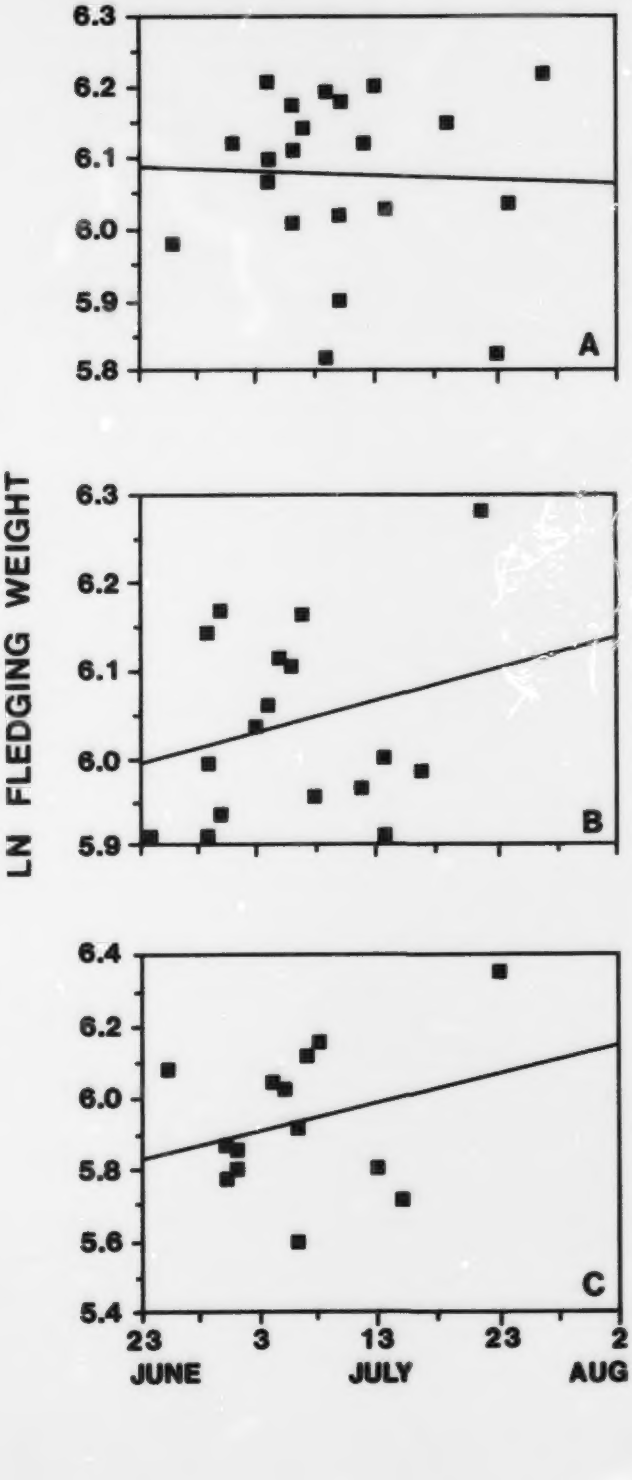
The difference in fledging success is even more striking and is due entirely to the large numbers of young chicks (less than one week old) that were eaten by wandering garter snakes (*Thamnophis elegans*) on Mitlenatch Island; there are no snakes on Mandarte Island. In light of this much lower reproductive success, it is interesting to note that significantly more one-egg clutches are laid on Mitlenatch Island (48/197 vs. 15/162, $\chi^2 = 13.14$, $P < 0.001$). This may be a result of a higher proportion of inexperienced breeders on Mitlenatch Island or of poorer feeding conditions around the island during the time when females are developing their eggs. It may also be a local adaptation towards maximizing lifetime reproductive success in an environment where there is high juvenile mortality and high adult survivorship (Horn and Rubenstein 1984).

Table 3
The effect of date on clutch size for Pigeon Guillemots on Mitlenatch Island, 1984–86

	1984			1985			1986	
Parameter	**26/5–1/6**	**2/6–8/6**	**8/6 +**	**28/5–4/6**	**5/6–9/6**	**10/6–17/6**	**1/6–12/6**	**13/6–24/6**
n	22	33	33	20	44	22	45	23
Proportion of one-egg clutches	0.05	0.21	0.36	0.10	0.27	0.32	0.16	0.48
P		<0.05			>0.10		<0.01	

[a] χ^2 tests performed on frequencies of one-egg and two-egg clutches within years.

Figure 2
The effect of hatching date on fledging weight of Pigeon Guillemot chicks on Mitlenatch Island, 1984–85. (A) Single chicks: $r^2 = 0.001$, $P = 0.875$. (B) Older chicks in two-chick nests: $r^2 = 0.058$, $P = 0.335$. (C) Younger chicks in two-chick nests: $r^2 = 0.077$, $P = 0.336$.



Egg predation on both Mandarte and Mitlenatch islands is probably exclusively by Northwestern Crows; it is unlikely that even the largest garter snakes on Mitlenatch Island are able to swallow guillemot eggs (Campbell 1969; P.W. Gregory, Univ. of Victoria, pers. commun.). On Mandarte Island, there is normally little or no chick predation, although in 1960 many well-grown chicks were killed by young Glaucous-winged Gulls (*Larus glaucescens*) (Drent *et al.* 1964).

Table 4 shows the effect of clutch size on reproductive success on Mitlenatch Island. In 1984, two-egg clutches were more productive than one-egg clutches, both in absolute terms and in terms of chicks fledged per egg laid. This was due largely to the much lower hatching success of single eggs as a result of intense predation. Hatching success was only slightly higher for two-egg clutches, but fledging success was substantially lower. As a consequence, the relative productivity of two-egg clutches was only half that of one-egg clutches. The reason for the difference is unclear, although it is possible that garter snakes, which hunt largely by using chemosensory cues (P.W. Gregory, pers. commun.), are able to detect two chicks much more easily than one.

Emms (1987) investigated whether the pattern of nest dispersion was related to predation intensity. Nests were highly clumped, but predation intensity did not vary with breeding density. This was true whether egg predation alone, chick predation alone, or total predation was being considered. However, in 1985, nearest neighbours between 10 and 20 m away from a depredated nest were more likely to be depredated than those less than 10 m away, indicating that on a very local scale there is an advantage to being close to other birds. A possible explanation for this is that snake predation on one nest satiates the snake for long enough to allow chicks in neighbouring nests to grow too large to be depredated once the snake starts hunting again. This, of course, presupposes that garter snakes are territorial, which is not known (P.W. Gregory, pers. commun.).

6.2. Chick growth and fledging

Guillemot chick growth follows a typical sigmoid growth pattern. Emms (1987) found that the logistic growth model fitted to log-transformed weight data gave the best fit to the growth curves of the majority (56.6%, $n = 53$) of chicks and used the asymptotic weight parameter A as a measure of fledging weight. Growth rate was measured as weight increase in grams per day in the middle of the fledging period. This is a better measure than the growth rate constant K of the logistic growth curve when comparing curves with different asymptotes (Hussell 1972; Gaston 1985).

Growth rate is influenced by brood size. Emms (1987) found that single chicks and the older chicks in two-chick broods had similar growth rates and fledging weights, but that younger chicks in two-chick broods had significantly lower fledging weights and growth rates than their older siblings. Drent (1965) found no such effect on Mandarte Island, although his comparison was simply a visual one, comparing average growth curves for chicks in one-chick and two-chick broods. Koelink (1972) found that second-hatched chicks suffered relative to their older siblings in 1969 and 1970, but not in 1971 (see Aitchison 1972). It is possible that year-to-year variation in the food supply caused these differences, although direct measures of fish stocks for guillemots are not available. Whether

Table 4
Reproductive success of Pigeon Guillemots in the Strait of Georgia

Location	Year	Clutch size	Mean clutch size	No. of clutches	Hatching success per egg	Eggs hatched per nest	Fledging success per chick	Chicks fledged per nest
Mandarte[a]	1957–59	1 and 2	1.91	111	0.62	1.18	0.90	1.08
	1960	1 and 2	1.90	51	0.59	1.12	0.41	0.46
Mitlenatch[b]	1984	1	1.00	21	0.43	0.43	0.44	0.19
	1984	2	2.00	70	0.73	1.46	0.48	0.70
	1984	1 and 2	1.76	91	0.69	1.21	0.47	0.57
	1985	1	1.00	27	0.37	0.37	0.50	0.19
	1985	2	2.00	79	0.47	0.94	0.20	0.19
	1985	1 and 2	1.74	106	0.45	0.78	0.24	0.19

[a] Data for Mandarte Island from Drent *et al.* (1964) and Drent (1965).
[b] Data for Mitlenatch Island from Emms (unpubl. data).

these differences in growth rates and fledging weights have fitness consequences for chicks is not known.

7. Conclusions

The breeding biology of the Pigeon Guillemot in the Strait of Georgia is essentially similar to that of the species elsewhere in its range. There are important differences between the two major breeding colonies in the Strait of Georgia. On Mandarte Island, almost all breeding sites are occupied each year, over 90% of the clutches are of two eggs, and fledging success is normally greater than one chick per nest (Drent *et al.* 1964; Drent 1965). On Mitlenatch Island, only about 50% of nest sites are occupied (although many nonbreeders are present early in the year), only 70–80% of clutches are of two eggs, and fledging success is much lower, largely because of intense predation on young chicks by garter snakes (Emms 1987, and unpubl. data). How these factors are interrelated is at present unclear, as we lack knowledge of important aspects of the ecology of the species. Demographic information is especially lacking, and long-term banding studies would provide a knowledge of such factors as juvenile survivorship, age at first breeding, the effect of age on clutch size and reproductive success, the degree of natal philopatry, and the age structure of the population. If this information is obtained, we may be able to explain the large differences in breeding biology in the two major breeding colonies in the Strait of Georgia and to better understand the selective pressures influencing the life history strategy of the species.

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Part 4

Populations and breeding ecology of shoreline birds

Introduction to the breeding ecology of shoreline birds in the Strait of Georgia

Robert W. Butler and Nicolaas A.M. Verbeek

1. Abstract

There are 26 species of breeding shoreline birds in the Strait of Georgia. Most species nest primarily in marshes (14), as well as in fields (9), trees (5), along rivers (5), in lakes or ponds (5), on or in seacliffs (2), and on beaches (2). The breeding avifauna of the Strait of Georgia is a mixture of estuarine and coastal species. When compared with the avifauna of the west coast of Vancouver Island, the Strait of Georgia has 22 unique species and 10 shared species.

2. Résumé

Vingt-six espèces d'oiseaux de rivage se reproduisent dans le détroit de Georgia. Elles nichent principalement dans les marais (14 espèces), mais aussi dans les champs (9), dans les arbres (5), sur les bords des cours d'eau (5), dans les lacs ou les étangs (5), dans les falaises ou sur celles-ci (2) ainsi que sur les plages (2). Il s'agit d'espèces estuariennes et côtières. L'avifaune du détroit compte 22 espèces absentes sur la côte ouest de l'île de Vancouver et 10 qui y sont présentes.

3. Introduction

Part 4 deals with shoreline birds, species that nest along the shore and that acquire most of their food from the intertidal and tidal areas of the Strait of Georgia. Seabirds, on the other hand, are those species whose normal habitat and food source are the sea (Part 3).

The habitats used by shoreline birds in the Strait of Georgia consist mostly of igneous rock interspersed with gravel and sand beaches, mudflats, and estuaries. Several of the beaches in the Strait of Georgia contain river-borne organic matter. Good examples exist at Boundary and English bays near Vancouver. Beaches along the northwest coast of the strait were formed by glacial deposits and resemble outer-coast beaches (Thomson 1981). Small beaches have formed throughout the strait from sand, gravel, and boulders eroded from nearby cliffs or bluffs.

A "beach" is a specific type of shore consisting of unconsolidated materials such as sand, gravel, and cobbles that extends from a physiographic change such as a seacliff or forest edge to the farthest point offshore where sediments can be carried by waves (Thomson 1981). Here, we have chosen the more common usage of beach as that area located between the highest high tide and the lowest low tide. Also included in our definition of shorelines are estuaries (see Butler *et al.*, this publication), seacliffs, rocky intertidal areas, sandspits, and lagoons. Seacliffs are vertical rock faces that reach 10 or more metres out of the sea along fjords and channels. Most consist of igneous rock; however, along the western shore of the Strait of Georgia, sedimentary rock cliffs have been undercut by wave action, unlike the igneous rock found elsewhere, which has eroded little. The erosion-resistant rocky beaches that typify the BC coastline extend along most of the Strait of Georgia. Most of the shore is covered in dense forest, here and there interspersed with suburban and recreational housing. Sandspits and lagoons have formed off some headlands in the strait; a particularly good example occurs on Sidney Island. In calm water, where mud has settled, eelgrass (*Zostera marina* and *Z. japonica*) beds are flourishing. Cutting across many of the coastal shores of the Strait of Georgia are over 200 creeks and rivers; some of these have formed deltas at their mouths, but most empty abruptly into the strait.

The most noticeable pattern in the annual cycle of many shoreline birds in the Strait of Georgia is the occurrence of immense populations in winter and their relative scarcity in summer. As long ago as 1792, Captain George Vancouver, upon entering the Strait of Georgia, remarked that "few of the feathered tribe were procured, although on our first arrival, [in April] the aquatic birds were so numerous that we expected a profuse supply of wildfowl . . ." (Pearse 1968).

The tremendous discharge from the Fraser River dilutes the salinity of the entire Strait of Georgia, creating estuarine conditions throughout the study area (Thomson 1981). Elsewhere (Butler *et al.*, this publication), we restricted our definition of an estuary for practical reasons to the proximity of river and creek mouths. However, when we compare the breeding shoreline avifauna of the entire Strait of Georgia with that on the west coast of Vancouver Island, the estuarine influence in the strait cannot be ignored. Hatler *et al.* (1978) reported only 10 "shoreline" species of birds breeding in Pacific Rim National Park on the west coast of Vancouver Island, whereas we found 26 breeding around the Strait of Georgia. Species common to both sites include the Red-throated Loon (*Gavia stellata*), Mallard (*Anas platyrhynchos*), Common Merganser (*Mergus merganser*), Bald Eagle (*Haliaeetus leucocephalus*), Osprey (*Pandion haliaetus*), Killdeer (*Charadrius vociferus*), Spotted Sandpiper (*Actitis macularia*), Belted Kingfisher (*Ceryle alcyon*), and Northwestern Crow (*Corvus caurinus*). Hatler *et al.* (1978) did not find nesting records for the Great Blue Heron (*Ardea herodias*) or Peregrine Falcon (*Falco peregrinus*), although they nest elsewhere on the exposed west coast. The remaining 15 species of breeding birds in the Strait of Georgia all occur in estuaries (Table 1) and mostly at the mouth of the Fraser River. Only the Northwestern Crow is confined to the BC coast. The breeding avifauna along the shoreline of the Strait of Georgia can best be described as a mixture of estuarine and coastal species.

Information gaps occur in our knowledge of most breeding shoreline birds in the Strait of Georgia. Unlike the seabirds (Vermeer, Part 3, this publication), the breeding biology of only five of the 26 species in the strait has been well documented. Little is known about the American Bittern (*Botaurus lentiginosus*), dabbling ducks, raptors, rails, most shorebirds, and Belted Kingfisher. Some species, such as the bittern, and rails are elusive, but many others are conspicuous components of the coastal avifauna.

The single major threat to shoreline breeding birds is the destruction of their habitats. The threat began about a century ago with the settlement by immigrants and the diking of the Fraser River delta (Butler and Campbell 1987), followed by clearcut logging of coastal forests after 1940. In the past 50 yr, the human population has spread around much of the Strait of Georgia from the urban centres of Vancouver, Victoria, Nanaimo, Courtenay, Campbell River, Powell River, and Sechelt. The population density around most of the strait, outside the urban centres, is 5.24 people per square kilometre (Fullard and Willett 1985). Much of the shoreline between Nanaimo and Campbell River and the Sunshine Coast is taken up by summer cottages and tourist resorts. As the Canadian

Table 1
Shoreline breeding bird species and their major habitats in the Strait of Georgia

	Habitats used		
Species	**Breeding**	**Feeding**	**Reference**
Red-throated Loon *Gavia stellata*	Lakes	Rocky shores, bays	Pearse 1946, 1954
Western Grebe *Aechmophorus occidentalis*	Estuarine marsh	Estuarine marsh	J. Ireland, pers. commun.
American Bittern *Botaurus lentiginosus*	Estuarine marsh	Estuarine marsh	Butler and Campbell 1987
Great Blue Heron *Ardea herodias*	Trees	Estuarine marsh, eelgrass beds, sandy and rocky beaches	Butler, this publication
Canada Goose *Branta canadensis*	Lakes, estuarine marsh, river edge, fields, coastal islands	Estuarine marsh, sea coasts	Dawe and Davies 1975; Vermeer and Davies 1978; J.N.M. Smith, pers. commun.
Mallard *Anas platyrhynchos*	Lakes, estuarine marsh, river edge, fields	Estuarine marsh	Butler and Campbell 1987
Northern Pintail *A. acuta*	Lakes, estuarine marsh, river edge, fields	Estuarine marsh	Butler and Campbell 1987
Blue-winged Teal *A. discors*	Fields, estuarine marsh edges	Estuarine marsh	Butler and Campbell 1987
Cinnamon Teal *A. cyanoptera*	Fields, estuarine marsh edges	Estuarine marsh	Butler and Campbell 1987
Northern Shoveler *A. clypeata*	Fields, estuarine marsh edges	Estuarine marsh	Butler and Campbell 1987
Gadwall *A. strepera*	Fields, estuarine marsh edges	Estuarine marsh	Butler and Campbell 1987
American Wigeon *A. americana*	Fields, estuarine marsh edges	Estuarine marsh	Butler and Campbell 1987
Hooded Merganser *Lophodytes cucullatus*	Tree cavity	Estuarine marsh, river	Butler and Campbell 1987
Common Merganser *Mergus merganser*	River edge	Estuarine marsh	Butler and Campbell 1987; British Columbia Wildlife Record Scheme
Osprey *Pandion haliaetus*	Tree	Rocky shores, bays	British Columbia Wildlife Record Scheme
Bald Eagle *Haliaeetus leucocephalus*	Tree	All beaches, estuaries	Vermeer, Morgan, Butler, and Smith, this publication
Northern Harrier *Circus cyaneus*	Estuarine marsh	Estuarine marsh	Butler and Campbell 1987
Peregrine Falcon *Falco peregrinus*	Seacliffs	All beaches, estuaries	pers. obs.
Virginia Rail *Rallus limicola*	Estuarine marshes	Estuarine marshes	Butler and Campbell 1987
Sora *Porzana carolina*	Estuarine marshes	Estuarine marshes	Butler and Campbell 1987
American Coot *Fulica americana*	Estuarine marshes, ponds	Estuarine marshes, ponds	Butler and Campbell 1987
Killdeer *Charadrius vociferus*	Fields	Mudflats, estuarine marshes, salt marsh, fields	Butler and Campbell 1987
American Black Oystercatcher *Haematopus bachmani*	Rocky and sandy beaches	Rocky and sandy beaches	Vermeer, Morgan, and Smith, Part 4, this publication
Spotted Sandpiper *Actitis macularia*	River edge, sandy beach	River edge, sandy beach	Butler and Campbell 1987
Belted Kingfisher *Ceryle alcyon*	Seacliff	All beaches	British Columbia Wildlife Record Scheme
Northwestern Crow *Corvus caurinus*	Trees, shrubs	Rocky and sandy beaches	Butler *et al.* 1984

population ages, more of the summer houses are becoming year-round residences for retired citizens, so that the pressure of the large summer tourist industry on breeding birds now extends throughout the year. That pressure manifests itself into habitat loss as a result of housing and deterioration of existing habitat because of human disturbance.

4. Breeding birds

As defined here, 26 species of shoreline birds nest around the Strait of Georgia (Table 1). Among these, 14 species nest in estuarine marshes, nine in fields, four in trees and one in tree cavities, five on lakes or ponds, two on beaches, and five on riverbanks. Two species nest on seacliffs. The shoreline birds in the Strait of Georgia are represented by more estuarine species than on the west coast of Vancouver Island. There are 22 breeding species in the strait that do not nest on the west coast and 10 species that are found at both locations (Table 1; Hatler *et al.* 1978). Most of the 22 species unique to the strait are waterfowl that breed in fresh or brackish water. LeBlond (this publication) describes the Strait of Georgia as a large estuary. Here, we review the published literature on waterfowl and the Northwestern Crow. New information on the breeding biology of the Great Blue Heron, Bald Eagle, and American Black Oystercatcher are presented later in Part 4.

4.1. Breeding biology of waterfowl

One goose and nine species of ducks regularly nest along the shores of the Strait of Georgia (Table 1). The largest nesting populations of all 10 species, except the Common Merganser, which nests along coastal streams (Wood 1984), occur in the Fraser River delta (Butler and Campbell 1987).

In contrast to the ducks, the Canada Goose (*Branta canadensis*) is a widespread and abundant nesting species. Canada Geese did not nest around the Strait of Georgia before 1940 (Munro and Cowan 1947; Dawe and Davies 1975). Starting in 1967, small numbers of geese from Ontario and the Canadian Prairies were released at various sites around the lower Fraser River valley. Today, the population in the lower Fraser River valley is estimated to be 8000 to 10 000 birds (D. Wilson, pers. commun.). Smaller numbers reside near Victoria, Duncan, Nanaimo, Courtenay, Campbell River, and Sechelt, but we could find no published information on the size of these nesting populations. One or two pairs nest on small islands in the southern strait, such as Mandarte and Imrie islands (J.N.M. Smith, pers. commun.).

There are two published studies of the breeding biology of the Canada Goose in the Fraser River delta (Dawe and Davies 1975; Vermeer and Davies 1978). In 1973, there were 300 free-flying Canada Geese at the George C. Reifel Migratory Bird Sanctuary (Dawe and Davies 1975), and about 120 pairs nested there in 1975 (Vermeer and Davies 1978). Geese nested in fields on islands, along ditches and sloughs, on small peninsulas, and on nesting platforms. Pairs visited man-made nest platforms in January, and eggs were laid from 15 March to 28 April. The peak of egg laying occurred in the first week of April (Vermeer and Davies 1978). Vermeer and Davies (1978) estimated that successive eggs were laid on average every 1.17 d until a mean clutch of 6.21 eggs was laid.

In 1975, most nests (47 of 56) hatched their eggs; the rest were lost to predators (three nests), abandoned (two), or disturbed by humans (two), or the goose died (two). Most (84.3%) eggs hatched ($n = 236$ eggs in 47 nests; Dawe and Davies 1975). In 1976, 89.3% of the clutches hatched.

The nesting duck populations are nowhere large, and little information exists on their breeding ecology in the Strait of Georgia. Most (about 90%) of the winter population (Butler *et al.*, this publication) nests outside the strait; the Mallard, Gadwall (*Anas strepera*), Cinnamon Teal (*A. cyanoptera*), and Blue-winged Teal (*A. discors*) are the most numerous breeders. The most abundant nesting ducks on the Alaksen National Wildlife Area in the Fraser River delta are the Mallard and the Gadwall. Butler and Campbell (1987) provided ranges in egg laying dates, clutch sizes, and hatching dates for the species that nest in the Fraser River delta. Most species lay their eggs between March and June and lead their broods into the estuary.

Mallards in the Fraser River delta lay eggs from 13 March to 17 July (Butler and Campbell 1987). This species also nests near ponds and in estuaries around the Strait of Georgia. A few pairs of Northern Pintail (*Anas acuta*) and Northern Shoveler (*A. clypeata*) that nest in the Fraser River delta lay eggs in April that hatch in late May. Blue-winged Teal and Cinnamon Teal are fairly common breeders in the Fraser River delta and the Little Qualicum River estuary (N. Dawe, unpubl. data). Eggs are laid from late May to mid-June. About 75 pairs of Cinnamon Teal nest in the Fraser River delta, and they have an average brood size of 6.8 ducklings from 3 June to 10 August (Butler and Campbell 1987). Gadwall numbers have increased on the coast since the mid-1960s (Crowell and Nehls 1966; Canning and Herman 1983) to about 100 pairs in the Fraser River delta in 1985 (Butler and Campbell 1987). Most eggs are laid from late May to early June, with replacement clutches being laid as late as July. The mean clutch size in 29 nests was 9.7 eggs (range = 8–13 eggs), and broods were seen as late as 14 August (Butler and Campbell 1987). No American Wigeon (*Anas americana*) nests have been found, but broods have been seen on the Fraser River delta.

4.2. Breeding biology of the Northwestern Crow

The Northwestern Crow resides along the northeastern Pacific coastal plain (Godfrey 1986) and is a ubiquitous species around the Strait of Georgia. Until 15 yr ago, little was known about the breeding ecology of this species, but today it is one of the most studied corvids in the world. Most of the breeding ecology of the Northwestern Crow has been researched on two islands at opposite ends of the Strait of Georgia. The earliest studies were done on Mandarte Island (48°38′N, 123°17′W) by Drent *et al.* (1964). Over a decade later, studies began on Mitlenatch Island (49°57′N, 125°00′W), followed by several studies on both islands (Verbeek and Butler 1981; Butler *et al.* 1984; Richardson *et al.* 1985).

Mandarte Island is a 700-m-long, rocky island at the southern end of the Strait of Georgia (Tompa 1964). It supports large populations of nesting seabirds (Drent *et al.* 1964). Mitlenatch Island is a 35-ha, sparsely vegetated island at the northern end of the Strait of Georgia (Brooke *et al.* 1983). Like Mandarte Island, Mitlenatch Island also supports large populations of breeding seabirds (Campbell 1976).

Crows have nested on Mitlenatch Island at least since 1963 (and probably much earlier), when the first BC Parks Branch naturalists estimated the breeding population at 30 pairs (van Tets 1963). In 1979, Howie Richardson (pers. commun.) located 65 nests in a summer-long search for all nests, and that number has changed little in the past 7 yr (NAMV, unpubl. data). About 12 to 20 pairs nest annually on Mandarte Island (Verbeek 1982).

Northwestern Crows on Mandarte and Mitlenatch islands build their nests on the ground, in shrubs, and in trees (Butler *et al.* 1984). Significantly more early nests (eggs laid prior to 27 April) than late nests are built on the ground on both islands (Butler *et al.* 1984). Nests in shrubs and trees are constructed on average 1.9 and 2.3 m above ground, respectively. However, low nests are not typical throughout the crow's range—we have seen nests at least 20 m off the ground in trees on the BC mainland. Usually new nests are built each year. In Vancouver, crows begin carrying nest material in mid-March. Nests on Mandarte and Mitlenatch islands were made from twigs and lined with red cedar bark, moss, sheep's wool, grass, gull feathers, paper, and crow feathers (Butler *et al.* 1984), which seems typical of nests we have seen elsewhere around the strait.

Female crows on Mandarte and Mitlenatch islands beg toward their mates on and off a small (0.5 ha) territory until the first egg is laid, whereupon they beg from the nest or its vicinity. Eggs in first clutches are laid from 16 April to 9 May, whereas second clutches are laid as late as 31 May. The mean clutch size is four eggs (Butler *et al.* 1984). No significant differences occurred in the relative abundance of clutch sizes on Mitlenatch and Mandarte islands, nor did the number of eggs decline significantly with the season (Richardson *et al.* 1985).

Incubation is the sole responsibility of the female, which spends most (86.0%) of each daylight hour on the nest. After an average of 18.3 d, the last laid egg hatches. From 72 to 78% of all eggs hatch. Females brood the nestlings for much of the first 10 d, then join the males in search of food, much of which is obtained on beaches (Verbeek and Butler, this publication). Nestling crows weigh about 15 g upon hatching and leave the nest 32 d later weighing an average of 305 g (Butler *et al.* 1984). However, they are unable to fly more than a few metres when they first leave the nest and clamber about in nearby branches for approximately two weeks. Then they venture from the nest tree to follow their parents to nearby feeding areas. On Mandarte Island, 51% of the nests fledged at least one nestling, whereas only 40% did so on Mitlenatch Island.

At some nests, a third crow, known as a "helper," assists in raising the nestlings (Verbeek and Butler 1981). The type of help varies between territorial defense, feeding the young, and caching food. In return, helpers are fed by the male territory holder and are allowed to forage on the adults' territory. Helpers were always yearlings (second year), and their assistance benefited the adults in producing more offspring than pairs without helpers.

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Breeding ecology and population trends of the Great Blue Heron (*Ardea herodias fannini*) in the Strait of Georgia

Robert W. Butler

1. Abstract

This paper reviews past studies and presents new data on the breeding biology of Great Blue Herons (*Ardea herodias fannini*) and examines their population trends in the Strait of Georgia.

2. Résumé

L'auteur passe en revue diverses études sur la reproduction du Grand héron (*Ardea herodias fannini*), présente de nouvelles données et examine les tendances de la population du détroit de Georgia.

3. Introduction

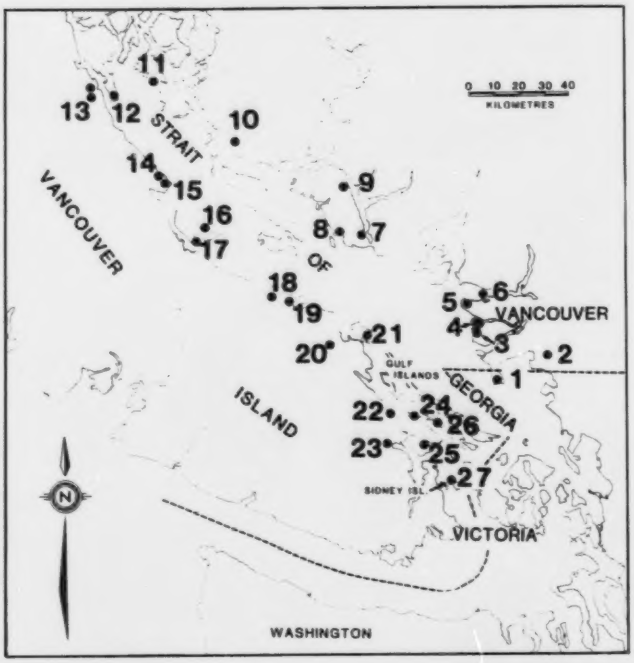
The breeding biology of the Great Blue Heron subspecies *Ardea herodias fannini*, which breeds on the BC coast, has been studied mostly in the past two decades (e.g., Paine 1972; Kelsall and Simpson 1980; Simpson 1984; Forbes *et al.* 1985*a*, 1985*b*; Simpson *et al.* 1987). The purpose of this paper is to review past studies and present new data on the breeding biology of Great Blue Herons and to examine their population trends in the Strait of Georgia.

4. Study area and methods

The breeding biology of the Great Blue Heron was studied in 1986–87 at a colony in Sidney Spit Marine Provincial Park (48°40′N, 123°20′W; hereafter referred to as Sidney). A description of the study area can be found in Butler *et al.* (1987). Sidney Island is one of the most southerly Gulf Islands in the Strait of Georgia (Fig. 1). It is mostly fringed by eroding sandstone cliffs, except at the western end, which is igneous rock, and the eastern end, which has a 96-ha lagoon and 2.3-km-long sand spit where most of the herons feed. The rest of the island is forested and mostly uninhabited.

I studied nesting herons at a colony in a red alder (*Alnus rubra*) woodlot at the southeast end of Sidney lagoon. On 22 March 1987, I numbered all trees that held nests from previous years at Sidney. In the first week of April, I noted which nests were occupied by adults and added new numbers as new nests appeared. Prior to and during egg laying, each nest was observed about once per week by moving very slowly around the edge of the colony. I recorded whether each nest was occupied by noting if an adult was standing or sitting in the nest. When the eggs began to hatch, I entered the colony every day to locate eggshells on the ground below nests. Over 90% of hatched eggshells are cast over the rim to the ground (Brandman 1976). It was not possible to tell which nests' eggshells fell from among nearby nests. In those cases, I determined which nest had the oldest young and then assigned hatching dates.

Figure 1
Location of nesting colonies of Great Blue Herons around the Strait of Georgia in 1987



Nests at colonies on the University of British Columbia (hereafter referred to as UBC) Endowment Lands in Vancouver and near Crofton on the west side of the Strait of Georgia were examined to determine clutch sizes. The length and breadth of collected eggs were measured with Vernier calipers. The volume and weight of eggs were estimated using the methods developed by Hoyt (1979).

Corvids typically puncture the sides of large eggs to carry them (Montevecchi 1976; pers. obs.). Egg predation by Common Ravens (*Corvus corax*) was quantified at Sidney by searching every 2–5 d for punctured shells within 500 m of the colony. Each shell was numbered, plotted on a map, and left where it was found. Two weeks after the last hatched egg was found in the colony, I searched for all shells by walking transects 10 m apart, covering the entire area within 500 m of the colony. The longer an eggshell stays on the ground, the greater the chance it will disappear. To estimate the accuracy of finding all eggs taken by corvids during ground searches, I divided the number of eggshells found on the postlaying transect (on 10 June) by the total number of eggshells found on regular searches through the egg stage and multiplied by 100%.

After the eggs hatched, I continued to visit the Sidney colony every few days to record the number of nestlings per nest and age of young herons found on the ground. I aged fallen nestlings by measuring culmen, tarsus, and wing lengths and using growth equations derived by Quinney (1982) for nestling Great Blue Herons in Nova Scotia. The number of young produced per nest was determined by counting the number of nestlings through a telescope and binoculars on several visits. I considered nestlings to have fledged when they clambered onto branches around the nest about 55 d after hatching. Comparisons of fledging success were made between nests that hatched young early (April–May) and late (June–July) in the season. I used the *G*-statistic (Zar 1984) to compare fledging success between early- and late-nesting pairs.

The number of colonies around the Strait of Georgia was determined mostly by volunteers. In February 1987, five teams of one or two observers were mailed descriptions of colony sites when last visited in 1979–81 (Forbes *et al.* 1985*b*). Each team searched all sites reported by Forbes *et al.* (1985*b*) and looked for new sites in their areas by recording the number of nests and colony locations on forms. Nestling production at some colonies was determined in late June or early July by the same volunteers. The number of active nests, defined as those with droppings on the nest trees or ground or young in the nest, were counted in all colonies. To determine the nestling production, a nest tree was chosen at random and the number of young was recorded for the nearest 30 active nests. In colonies with fewer than 30 nests, as many nests as possible were recorded. Those data were used to determine the number of breeding pairs (= number of active nests), proportion of successful nests (percentage of nests with at least one fledgling), and the mean number of young fledged per successful nest. In addition, a public request was run in newspapers for information on colonies on the BC coast in the autumn of 1987 (P.E. Whitehead, unpubl. data).

5. Breeding biology

Great Blue Herons return to their colonies in early spring. At Sidney Island on 22 March 1987, 53 (60.9%) out of 87 nests from the previous year were occupied, and no new nests were present. By 13 April, 71 nests were occupied, of which 11 were newly built and 60 were refurbished. By the end of the breeding season, 86 nests from previous years had been reused, and 33 new ones were constructed, for a total of 119 nests.

Four recently fallen but intact nests at Sidney Island were dismantled and weighed. There were 92, 122, 136, and 171 large (pencil-sized) twigs in the four nests. The nests were lined with small twigs. The total weights of those nests were 2570, 2600, 2800, and 4820 g.

Great Blue Herons on the south coast of British Columbia nest in a variety of trees. Simpson (1984) listed red alder, broadleaf maple (*Acer macrophyllum*), Douglas fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), lodgepole pine (*Pinus contorta*), and western red cedar (*Thuja plicata*). Forbes *et al.* (1985*b*) included arbutus (*Arbutus menziesii*) and bitter cherry (*Prunus emarginata*). In 1987, 388 nests were counted in colonies at Crofton, Gabriola, Nanaimo, Parksville, BC Forest Products, Powell River, and Sidney Island (see Fig. 1 for colony sites). Most (73.2%) were in red alder, 13.1% in Douglas fir, 12.4% in arbutus, 0.7% in garry oak (*Quercus garryana*), and 0.2% each in western hemlock and willow (*Salix* sp.). Although herons do not seem to be fussy about which tree species they will nest in, colonies seem to relocate in the same forest type (deciduous vs. coniferous) (Forbes *et al.* 1985*b*) and tend to choose a single tree species when other species occur in the same woodlot (Kelsall and Simpson 1980).

The location and number of nests per tree vary presumably in response to the tree's structure. Nests are built in the canopy of alders, but in large conifers several nests are often built on limbs up a single tree. Most alders support only one nest. At Sidney Island in 1986, 43 trees had single nests, and eight trees held two nests each. Of those 59 nests, 66.1% were built in the tree's crown, 27.1% on lower limbs, and 6.8% against the tree trunk. At the UBC colony, 41 of 57 trees had single nests, 13 had two nests, and three held three nests. Of those 76 nests, 55.3% were in the crown, 26.3% on tree limbs, and 18.4% against tree trunks. Both Sidney and UBC heron colonies were in red alders. The Crofton colony is in a variety of tree species, which makes it an anomaly among other colonies on the BC coast. Of 59 nests, 21 were in Douglas firs and 38 in arbutus. There were only two trees with single nests; other trees held two, three, four, five, six, eight, and nineteen nests.

Egg laying begins in early April. By back-dating for a 27-d incubation period (Vermeer 1969) from when the first eggshell was found below the nests (Bayer and McMahon 1981) in the Sidney Island colony in 1987, I estimated that 11.5% of the nests held eggs between 1 and 7 April, 29.9% between 8 and 14 April, 19.5% between 15 and 21 April, and 14.9% between 22 and 28 April. A further 24.1% of the nests held eggs between 29 April and 19 June (Fig. 2).

The length and breadth of 26 eggs from four colonies in 1986 were 6.4 cm (SD = 2.2) and 4.6 cm (SD = 1.4). The estimated mean volume of those 26 eggs was 6.9 cm^3, and the estimated mean fresh egg weight was 74.2 g (Hoyt 1979). The eggs of the subspecies *A. h. fannini* are the third largest in volume and weight of the six subspecies in North America (Table 1). The mean clutch size from 23 nests at UBC was 4.2 eggs (SD = 0.6) (P.E. Whitehead, unpubl. data), and 3.9 eggs (SD = 0.6) from 50 nests at Crofton.

The only known egg predator at Sidney was the Common Raven, which made daily forays to the colony. On three occasions, ravens were seen carrying heron eggs from the colony. In one of those cases, the raven cached the egg in debris along the forest edge and departed. The following day an eggshell was found about 3 m from the cache site. Twenty-six (89.7%) out of 29 numbered eggshells found on the forest floor were located on transect searches. That suggests that eggshells remained where the eggs were eaten for several weeks,and the intensive search located

Figure 2
Timing of hatching of Great Blue Heron eggs at Sidney Island in 1987

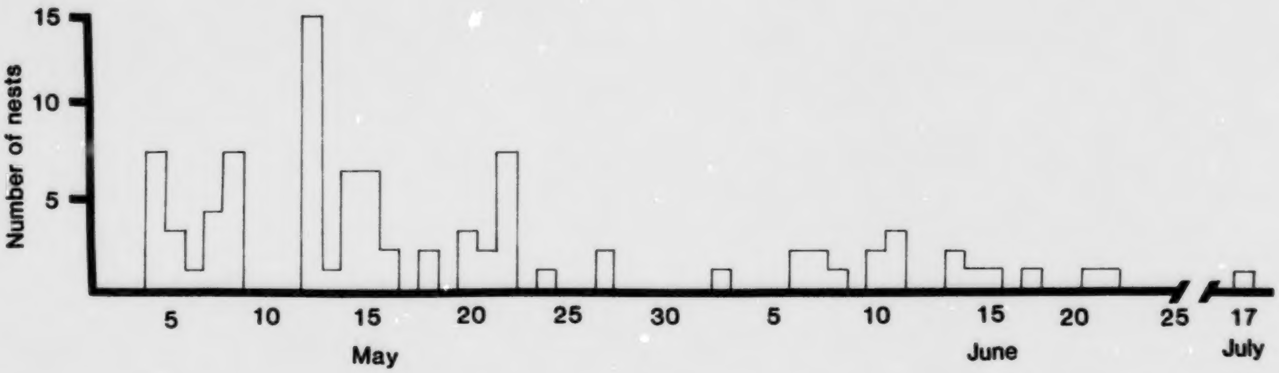


Table 1
Egg volumes of the six subspecies of Great Blue Herons in North America

Subspecies	Egg dimensions[a]		Volume (cm^3)[b]	Fresh weight (g)[c]
	Length (cm)	Breadth (cm)		
herodias	6.5	4.6	7.0	75.4
wardi	6.6	4.7	7.4	79.9
treganzai	6.5	4.5	6.7	72.1
hyperonca	6.3	4.5	6.5	69.9
sancti-lucae	6.1	4.5	6.3	67.7
fannini	6.4	4.6	6.9	74.2

[a] Data for *fannini* are from this study; all other data are from Palmer (1978).
[b] Volume = 0.51 LB^2, where L = length and B = breadth of eggs (Hoyt 1979).
[c] Fresh weight = 0.548 LB^2, where L = length and B = breadth (Hoyt 1979).

most shells. Four new eggshells were located around the colony, and two were removed by us from the ground in the colony, making a total of 35 eggs known to have been predated. If the intensive search located 89.7% of the predated eggs, then an estimated 10.3% (4.0 eggs) were missed, making a total of 39 eggs taken by ravens. An assumption of a mean clutch size of 4.1 eggs in 85 nests known to have eggs prior to the intensive search results in a total of 349 eggs, of which an estimated 39 (11.2%) eggs were taken by ravens.

As the season progressed, dead and living nestlings were found on the ground at Sidney (13 in 1986, 19 in 1987) and at UBC (14 in 1986). Three nestlings were 5–10 d old, 10 nestlings were 11–20 d old, 13 were 21–30 d old, and 10 were 31–40 d old. The average age was 24.3 d (SD = 9.4). Many more could have fallen and either wandered away or been carried off by scavengers. At Sidney I have seen river otters (*Lutra canadensis*), Common Ravens, and Turkey Vultures (*Cathartes aura*) eating fallen nestling carcasses. Two dead nestlings that were still warm when found disappeared within 24 h, whereas many others remained for days or weeks.

Fledging success declined as the nesting season progressed. Early (before 1 June) nests produced significantly ($P < 0.001$) more fledglings than late nests (G = 11.628, df = 3, $P < 0.001$). That is partly a result of the higher number of unsuccessful nests; 19.9% of early nests that hatched eggs were unsuccessful, versus 47.1% of late nests. However, when unsuccessful nests are removed from the calculations, early nests did not produce significantly more young than late nests (G = 4.605, df = 3, $P < 0.05$). These calculations are based upon all 85 nests in the Sidney colony. The mean fledging success for the Sidney colony was 2.3 young per successful nest (SD = 0.6; n = 48).

The number of young produced in several colonies around the Strait of Georgia has been gathered for several years (Table 2). The mean production of the number of young produced per year has declined at a rate of 0.1 young per successful nest each year (Fig. 3).

6. Population trends

In 1987, volunteers helped locate 1027 nests in 27 colonies around the Strait of Georgia (Fig. 1, Table 3). The largest colonies were found around the Fraser River delta and southern Gulf Islands. Of the 27 sites reported in use in 1979–81 by Forbes *et al.* (1985*a*), only 11 (40.7%) were still in use in 1987. In total, 85 sites are known to have been used since records began at the start of this century. Only a few colony sites have been used repeatedly for many years. For example, the site at Stanley Park dates back to at least 1921 (Racey 1921*a*, 1921*b*); Point Roberts was in use in 1948 (Forbes *et al.* 1985*a*); and Sidney Island has been used annually since at least 1961 (F. Flint, pers. commun.).

The three colonies for which data on the number of nesting pairs are available over the last decade (Stanley Park, UBC, and Point Roberts) changed as much as 14.1% between years (1977–78). The pooled number of nesting pairs in those colonies by year are as follows: 1977—371 pairs; 1978—432 pairs; 1979—434 pairs; 1980—407 pairs; 1981—411 pairs; and 1987—400 pairs (Simpson 1984; Forbes 1985*b*; RWB, unpubl. data). The data are scant earlier this century, but counts in the intermittent years at three colonies suggest that populations have fluctuated about 20% over the years. The mean

Table 2
Annual production of nestlings per successful nest of Great Blue Herons at six colonies in the Strait of Georgia

Colony	Year	No. of young/ successful nest[a] Mean	SD	n	Reference
Point Roberts	1987	2.4	0.7	29	This study
	1986	2.4	0.8	25	This study
	1981	2.4	ND[b]	50	Forbes *et al.* 1985*a*
	1980	2.9	ND	53	Forbes *et al.* 1985*a*
	1979	2.9	ND	33	Forbes *et al.* 1985*a*
	1978	2.5	ND	39	Forbes *et al.* 1985*a*
	1977	2.8	ND	39	Forbes *et al.* 1985*a*
Nicomekl[c]	1987	2.3	0.7	29	This study
	1986	2.1	0.8	12	This study
	1985	3.2	0.6	15	L.S. Forbes, pers. commun.
	1980	2.3	ND	22	Forbes *et al.* 1985*a*
	1979	3.1	ND	13	Forbes *et al.* 1985*a*
	1978	2.8	ND	17	Forbes *et al.* 1985*a*
	1977	2.9	ND	18	Forbes *et al.* 1985*a*
University of British Columbia	1987	2.0	0.8	141	P.E. Whitehead, unpubl. data
	1986	2.0	0.9	46	This study
	1981	1.9	ND	42	Forbes *et al.* 1985*a*
	1980	2.4	ND	51	Forbes *et al.* 1985*a*
	1979	2.9	ND	22	Forbes *et al.* 1985*a*
	1978	2.8	ND	30	Forbes *et al.* 1985*a*
	1977	2.9	ND	23	Forbes *et al.* 1985*a*
	1971	2.7	1.0	38	J.R. Krebs, unpubl. data
Stanley Park	1981	2.2	ND	9	Forbes *et al.* 1985*a*
	1980	2.1	ND	19	Forbes *et al.* 1985*a*
	1979	2.4	ND	ND	Forbes *et al.* 1985*a*
	1978	2.6	ND	22	Forbes *et al.* 1985*a*
	1977	2.3	ND	12	Forbes *et al.* 1985*a*
Crofton	1986	2.0	0.7	13	This study
Sidney Island	1987	2.3	0.6	54	This study
	1986	2.2	0.9	27	This study
Colony mean		**2.5**	**0.4**	**28 colony years**	

[a] A successful nest raised one or more young to fledging age.
[b] Not determined.
[c] The Nicomekl colony is the same as Crescent Beach in Forbes *et al.* (1985*a*).

Figure 3
Mean number of fledgling Great Blue Herons produced from active nests (raised at least one nestling) in the same colonies between 1977 and 1987

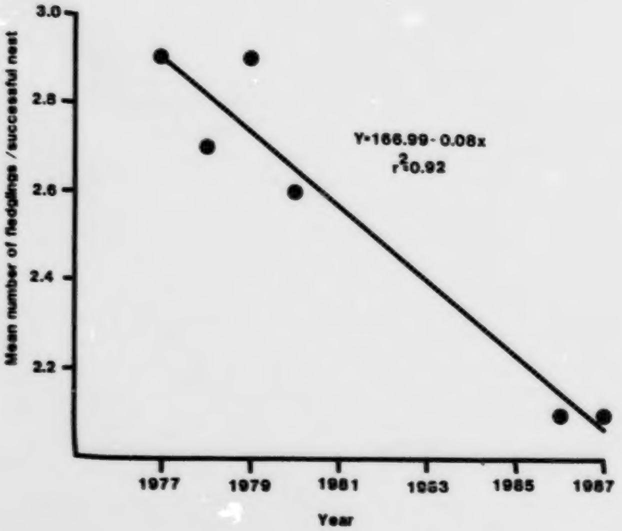


Table 3
The number of nests in Great Blue Heron colonies in the Strait of Georgia in 1987

Colony No.	Name	No. of nests	No. of active nests
1	Point Roberts	253	183
2	Nicomekl	59	28
3	Lulu Island	4	ND[b]
4	Delta Inn	7	7
5	University of British Columbia	214	158
6	Stanley Park	31	16
7	Sechelt	6	ND
8	Halfmoon Bay	3	ND
9	Kleindale	11	ND
10	Powell River	44	ND
11	Whaletown	8	ND
12	Cape Mudge	8	2
13	BC Forest Products	13	ND
14	Little River (Vega. Ct.)	27	ND
15	Little River (Butler Rd.)	4	ND
16	Hornby Island	7	ND
17	Denman Island	35	4
18	Parksville	24	24
19	Nanoose	1	1
20	Nanaimo	20	ND
21	Gabriola	94	3
22	Crofton	93	60
23	Duncan	25	25
24	Ganges	ND	ND
25	Fulford Harbour	1	ND
26	Prevost	14	ND
27	Sidney	100	85
Total		**987**	

[a] Colony numbers correspond to locations in Figure 1.
[b] Not determined.

number of nests at Point Roberts since 1948 was 196 (SD = 44.2, $n = 9$ yr); at UBC since 1970 was 105 (SD = 37.6, $n = 9$); and at Stanley Park since 1921 was 31 pairs (SD = 6.7, $n = 17$). In 1987, three colonies (Crofton, Gabriola, and Denman) failed completely. The losses occurred in the egg stage at Crofton and Denman, and in the nestling stage at Gabriola. Losses of this degree have never been reported in British Columbia.

7. Discussion

The reproductive success of Great Blue Herons on the southwest coast of British Columbia has been examined by Forbes *et al.* (1985*a*), who found a mean fledging rate of 2.5 young per successful nest in 14 colonies between 1977 and 1981. That is slightly higher than the 2.0–2.4 range I found in six colonies in 1986–87. However, interyear comparisons within colonies revealed a fairly wide range in annual production rates. For example, Point Roberts and Stanley Park varied by 0.5 per successful nest, and Nicomekl and UBC by 1.0 young.

Pratt and Winkler (1985) also found that the number of fledglings produced per nest varied between years in California. Clutch size and time of breeding also affected the production of young in their study. They calculated that 46.8% of eggs resulted in fledged young. Assuming that the clutch size at Sidney is similar to those at Crofton and UBC (4.0 eggs), then 340 eggs were laid in 85 active nests. Seventy-four of those 85 nests produced 170 young, so 50% of the eggs laid resulted in fledged young, which is very close to Pratt and Winkler's figure of 46.8%.

The number and distribution of colonies have changed around the Strait of Georgia since the censuses of Simpson (1984) and Forbes *et al.* (1985*b*). However, Simpson (1984) examined colonies only on the east side of the strait, and Forbes *et al.* (1985*b*) compiled only historical records; no strait-wide census was made. Nevertheless, many sites reported in use 7–10 yr ago were abandoned in 1987. In contrast, the three largest colonies at Sidney, Point Roberts, and UBC have more or less maintained a stable number of breeding pairs, as has the much smaller Stanley Park colony. The reasons for abandonment at some sites and strong fidelity at others are unclear. Human disturbance, especially early in the breeding season, has been strongly implicated as a cause of abandonment at some colonies (Kelsall and Simpson 1980; Vos *et al.* 1985). Raptors nesting nearby might also cause abandonment (Kelsall and Simpson 1980). However, that does not mean that Great Blue Herons are intolerant of nearby human or raptor activities. The colony at Stanley Park has nested in trees above the zoo for years with no apparent negative effects. Similarly, Webb and Forbes (1982) documented a colony established in trees alongside a busy access road and major hotel near the Vancouver International Airport. The Sidney colony is located in the Gulf Islands, where the Bald Eagle population has doubled in the past decade or so (Vermeer, Morgan, Butler, and Smith, this publication).

A crude comparison of the number of breeding Great Blue Herons around the Strait of Georgia can be made using data on the number of nests in all colonies in the last decade. About 1000 nests of Great Blue Herons were found around the Strait of Georgia in 1987. Using colony totals from Forbes *et al.* (1985*b*) for the same area in 1979–81, there were about 1100 pairs of breeding herons.

Forbes *et al.* (1985*b*) estimated that Great Blue Herons in British Columbia would maintain their populations if 80% of the nests raised 2.4 young and if mortality rates (Henny 1972) remained unchanged. That estimate is a little high, because 93.0% ($n = 469$ nests in five colonies) of the nests are successful in the Strait of Georgia, instead of 80% assumed by Forbes *et al.* (1985*b*). I estimate that a stable population will be maintained if 2.2 young are produced per successful nest, assuming the same mortality rates calculated by Henny (1972), whose mortality schedule was based upon band recoveries from Great Blue Herons across North America. Forbes *et al.* (1985*a*) showed that mortality among nesting Great Blue Herons was higher at high latitudes than at low latitudes. Herons are nonmigratory in the Strait of Georgia (Palmer 1978) and may have very different rates of mortality compared with herons in other parts of North America.

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Population and nesting habitat of American Black Oystercatchers in the Strait of Georgia

Kees Vermeer, Ken H. Morgan, and G.E. John Smith

1. Abstract

The nesting population of American Black Oystercatchers (*Haematopus bachmani*) was censused, and their island and nest site habitat was investigated in the Gulf Islands in 1987. Of 284 islands surveyed, 36 had nesting pairs, with an average of 1.4 pairs per nesting island. Overall breeding pair density on the 284 islands was 0.06 pairs per kilometre of shoreline, compared with 3.7 pairs per kilometre of shoreline on the 36 nesting islands.

Islands used by oystercatchers were significantly smaller, had more bare ground, were less forested, and were inhabited by fewer people than nonnesting islands, but they were significantly more inhabited by Glaucous-winged Gulls (*Larus glaucescens*). Nests averaged 7.08 ± 4.38 m away from, and 2.23 ± 1.63 m above, the high-tide line and 0.73 ± 1.44 m from the nearest land vegetation. Nests tended to be close to elevated logs or rocks and on relatively gentle slopes. Although nesting with gulls may have been beneficial in the past, extensive predation by gulls and their recent invasion of oystercatcher habitat suggest that the association of the two species may no longer be beneficial to the oystercatchers.

2. Résumé

La population nicheuse de l'Huîtrier noir (*Haematopus bachmani*) ainsi que son habitat insulaire et de nidification ont été étudiés dans les îles Gulf en 1987. Sur les 284 îles examinées, 36 abritaient des couples qui nichaient; le nombre moyen de couples par île de nidification était de 1,4. La densité globale des couples s'élevait à 0,06 couple par kilomètre du littoral pour les 284 îles et à 3,7 pour les 36 îles de nidification.

Les îles utilisées par les Huîtriers noirs étaient nettement plus petites, plus dénudées, moins boisées et moins peuplées que les îles non utilisées pour la nidification, mais elles comptaient nettement plus de Goélands à ailes grises (*Larus glaucescens*). Les nids se trouvaient en moyenne à 7,08 ± 4,38 m de la limite des marées hautes, à 2,23 ± 1,63 m au-dessus du niveau des marées hautes et à 0,73 ± 1,44 m de la végétation terrestre la plus proche. En général, les nids étaient situés près de hautes billes ou roches et sur des pentes relativement plus douces. La cohabitation avec les goélands et mouettes a peut-être été bénéfique par le passé, mais elle ne semble plus l'être, car les Huîtriers noirs sont victimes d'une prédation importante par ceux-ci et ont vu récemment leur habitat envahi par ces derniers.

3. Introduction

American Black Oystercatchers (*Haematopus bachmani*), for convenience called Black Oystercatchers here, nest on barren rocky shores (predominantly islands) just above the high-tide line. Their breeding range extends from the western Aleutian Islands in Alaska to central Baja California, Mexico. The Black Oystercatcher is found in relatively low numbers along the Pacific coast, is a resident, and restricts its feeding to the rocky intertidal region. Although several studies on the feeding behaviour and nesting biology of Black Oystercatchers have been made on the west coast of Vancouver Island (Hartwick 1974, 1976, 1978; Groves 1982, 1984) and on the west coast of Washington State (Nysewander 1977), there is little information on the biology of the species in the Strait of Georgia. Drent *et al.* (1964) investigated the nesting of Black Oystercatchers on Mandarte Island and Race Rocks in the Strait of Georgia (Figs. 1 and 2). Oystercatchers laid eggs mostly during May, with replacement clutches initiated as late as 5 July. Clutch size averaged 2.5 eggs, and incubation lasted about 27 d. Young oystercatchers remained with adults into September. Each pair produced an average of 0.7 young per season. The major cause of egg loss was predation by Northwestern Crows (*Corvus caurinus*). Hartwick (1974) observed a much lower reproductive success of Black Oystercatchers (an average of 0.2 young per nest in 1971 and 0.3 young in 1972) on Cleland Island, on the west coast of Vancouver Island. The low reproductive success on Cleland Island resulted mainly from predation by Northwestern Crows and Glaucous-winged Gulls (*Larus glaucescens*) and summer storms that washed out nests or drowned chicks. Nysewander (1977) reported that Black Oystercatchers produced 0.4 and 1.4 young per pair on Destruction Island, on the west coast of Washington State, in 1974 and 1975, respectively. The most important sources of natural mortality on Destruction Island were the same as those on Cleland Island.

Although the above authors provided data on the feeding behaviour and nesting biology of Black Oystercatchers, little is known about the birds' selection of nesting habitat. We also have no information at all on the species' nesting population in the Gulf Islands or elsewhere in the Strait of Georgia. For these reasons, we set the following objectives:

Figure 1
Distribution of nesting sites of Black Oystercatchers in the northern section of the Strait of Georgia and on Race Rocks. Numbered colonies are identified in Table 1.

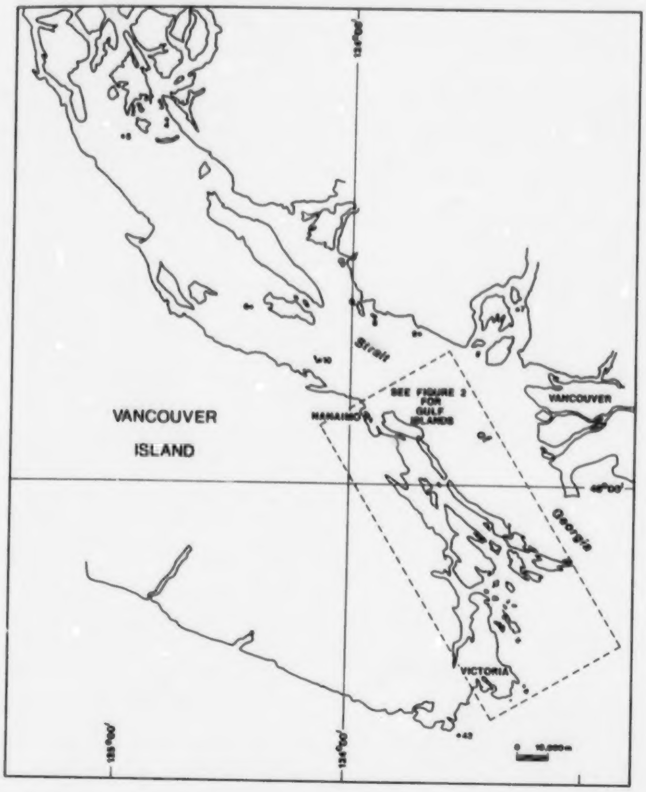
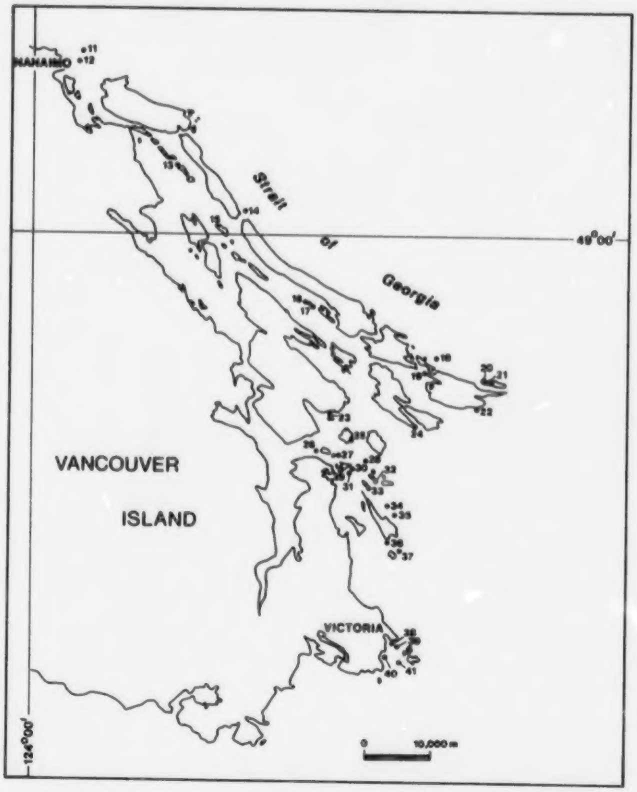


Figure 2
Distribution of nesting sites of Black Oystercatchers in the Gulf Islands. Numbered colonies are identified in Table 1.



(1) to determine the nesting population of Black Oystercatchers in the Gulf Islands;
(2) to determine which islands and sites the birds select for nesting in the Gulf Islands; and
(3) to obtain general information on the nesting status of the species in the Strait of Georgia north of the Gulf Islands.

4. Methods

4.1. Surveys and measurements

We surveyed the Gulf Islands from Hudson Rocks near Nanaimo to the Chain Islands near Victoria (Table 1, Fig. 2) for nesting oystercatchers between 5 and 23 June 1987. We circled all islands ($n = 284$) by motorboat and landed on any island on which we observed oystercatchers. We searched these islands on foot to obtain evidence of nesting, such as presence of nests or young; in their absence, we tried to determine if the birds' behaviour indicated nesting. We also censused 30 islands north of the Gulf Islands for nesting oystercatchers on 8 and 9 July, as well as the five islets that compose Race Rocks in the Strait of Juan de Fuca on 15 July 1987 (Table 1, Fig. 1) during surveys of other seabirds.

In the Gulf Islands, the percentage of bare ground (low herbaceous cover or bare rock) and extent of forestation (>50% = forested) were noted for each island. Observations were also made on the presence of nesting Glaucous-winged Gulls and the inhabitation of islands by people. We measured the area and perimeter of all islands from charts with a planimeter. When we found nests, we measured their distance to and above the high-tide line (the upper limit of the barnacle zone), to the nearest land vegetation, to the nearest elevated rock or log (≥ 10 cm), and to the nearest gull nest. We also measured the microslope of each nest substrate; this was determined from the average maximum slope over a 30-cm distance. Except for distance to and height above the barnacle zone, we also measured the same variables for points 2 m away from nests (matched points). Matched points were selected randomly from one of 12 compass points. The distance of 2 m was arbitrarily chosen.

4.2. Statistical analysis

The statistical analyses done in this paper relate mainly to comparisons of nesting with nonnesting islands (Table 2), and of nesting sites with matched nonnesting sites (Table 3). The distribution of the data that are summarized in these tables is highly skewed, with nonhomogeneous variances. Because comparisons of means could not be carried out using classical two-sample *t*-tests, *F*-tests, or even some nonparametric tests, inferences about equality of the medians and the distributions were made using two-way chi-square contingency tables. The means and standard deviations are presented for descriptive purposes.

For each variable in Table 2, the islands were divided into two or three categories with approximately the same number of islands in each. Then, a two-way contingency table was prepared to test for significant differences.

Table 1
Islands with nesting Black Oystercatchers in the Strait of Georgia, 1987

Location[a]	No. of islands	No. of islands with nests	No. of nesting pairs
1. Three Islets	3	1	1
2. Little Rock	1	1	1
3. Powell Islets	2	2	2
4. Major Islet	1	1	1
5. Mitlenatch Island and Islet	2	1	2
6. Sister Islets	3	1	1
7. Christie Islets and Pam Rock	3	1	2
8. Merry Island	1	1	1
9. White Islets	2	2	2
10. Ballenas Islands	2	1	1
11. Five Finger Island	1	1	3
12. Hudson Rocks	4	2	2
13. Ruxton Islets	2	1	1
14. Canoe Islet	1	1	1
15. Rose Islets	4	3	3
16. Ballingal Islets	2	1	1
17. Unnamed islet	1	1	1
18. Belle Chain Islands	3	1	3
19. Minx Reef Rock	1	1	1
20. Pine Island	1	1	2
21. Cabbage Island	1	1	1
22. Java Islets	2	2	4
23. Unnamed islet	1	1	1
24. Unnamed islet	1	1	2
25. Tortoise Islets	2	1	1
26. Arbutus Island	1	1	1
27. Pym Island	1	1	1
28. Imrie Island	1	1	2
29. Unnamed islet	1	1	1
30. Dock Island	1	1	1
31. Unnamed islet	1	1	1
32. Rubly Island	1	1	1
33. Unnamed islet	1	1	1
34. Mandarte Island and Islet	3	2	3
35. Halibut Island	1	1	2
36. Sallas Rocks	3	1	1
37. Little D'Arcy Islets	2	1	1
38. Flower Island	1	1	1
39. Jemmy Jones Island	1	1	1
40. Mary Tod Island	1	1	1
41. Chain Islands	23	2	4
42. Race Rocks	5	2	3
Total	**95**	**51**	**67**

[a] Numbered locations are shown in Figure 1.

The data in Table 3 were paired by site (nest site vs. matched point). Differences were calculated, and a chi-square test was used to determine whether the number of positive differences was significantly different from the number of negative ones.

5. Results

5.1. Population

We observed that 51 of 319 islands (15.7%) surveyed in the Strait of Georgia (including the Gulf Islands) had nesting pairs of oystercatchers. These 51 islands had a total of 67 pairs, or an average of 1.3 pairs per island (Table 1). Of the 284 islands surveyed in the Gulf Islands, 36 (12.7%) had 51 breeding pairs, an average of 1.4 pairs per nesting island. The shoreline of the 284 islands was 848 km long, and that of the 36 nesting islands 13.7 km, indicating a breeding pair density of 0.06 and 3.7 nests per kilometre of shoreline, for all islands and nesting islands, respectively.

5.2. Island habitat and nest sites

Islands used by nesting oystercatchers had a greater percentage of bare ground, were smaller, were less forested, were less inhabited by people, and were more frequently used by nesting Glaucous-winged Gulls than were nonnesting islands (Table 2).

Thirty-two nests of oystercatchers averaged 7.08 ± 4.38 m away from, and 2.23 ± 1.63 m above, the barnacle zone, and 0.73 ± 1.44 m from the nearest land vegetation. Comparison of nest sites with their matched points indicates that nests were closer to elevated logs or rocks, whereas their matched points were on significantly steeper slopes (Table 3). Predominant nest materials of oystercatchers were grey rock chips and white shells and bones (Table 4).

6. Discussion

6.1. Population

Little has been published on the status of Black Oystercatchers in the Gulf Islands, so no population comparisons can be made. However, we can compare nesting densities there with those for the species in the San Juan Islands, which are part of the same island chain as the Gulf Islands. Nysewander (1977) estimated that the nesting population of Black Oystercatchers in the San Juan Islands (based on breeding season counts) consisted of a maximum of 89 individuals, or about 45 pairs. We calculated the total shoreline of the San Juan Islands, as surveyed by D.R. Nysewander (pers. commun.), to be 652 km, and that of nesting islands, 115 km. Corresponding nesting densities for oystercatchers for these categories were found to be 0.07 and 0.39 pairs per kilometre of shoreline, respectively. Overall oystercatcher densities in the Gulf and San Juan islands are therefore almost identical. The difference in nesting island densities between the island groups relates to one pair of oystercatchers occurring on one large island (Lopez) in the San Juan Islands. Without Lopez Island, the average oystercatcher density in the San Juan Islands was 2.1 pairs per kilometre of nesting island, which is similar to the 3.7 pairs per kilometre that we observed in the Gulf Islands.

6.2. Island habitat and nest sites

It is not surprising that Black Oystercatchers nest on relatively small islands with few trees in the Gulf Islands. Most of the large forested islands have villages or residences with cats and dogs and undoubtedly established populations of wild predators (e.g., river otters [*Lutra canadensis*]; Vermeer, Morgan, Butler, and Smith, this publication), which could prey upon eggs, chicks, and possibly adults. The presence of nesting Glaucous-winged Gulls may indicate to oystercatchers a site relatively safe from mammalian predators, although gull colonies are now more frequently visited by river otters than in the past (Vermeer and Devito, this publication). Alarm calls of gulls can also serve as a warning of approaching predators. Both Hartwick (1974) and Nysewander (1977) suggested that the nesting of oystercatchers near gull nests reduced crow predation on oystercatchers.

The nesting of oystercatchers near elevated objects, whether logs or rocks, could be related to the need of incubating or brooding birds and their nests for protection from the sun, prevailing wind, and/or predators. Measurements of compass bearings of the nearest elevated logs or rocks, however, were similar for both nests and matched points, suggesting that concealment from predators is a more important factor in nest selection.

Table 2
Comparison of variables of islands with (n = 36) and without (n = 248) nesting Black Oystercatchers in the Gulf Islands, 1987

Variables	Nesting islands			Nonnesting islands			Significance		
	Mean ± SD	Median	%	Mean ± SD	Median	%	χ^2	df	P
Island area (ha)	1.16 ± 1.62	0.3		127 ± 614	1.3		13.03	2	0.005
Island perimeter (m)	385 ± 378	250		3351 ± 11 889	465		13.35	2	0.004
Bare ground (%)	81 ± 26	97.5		55 ± 40	75		16.40	2	0.001
Forested islands			11.1			44.0	12.94	1	0.000
Inhabited by people			8.3			28.2	5.18	1	0.023
Nesting gulls present			55.6			17.3	24.26	1	0.000

Table 3
Means, standard deviations, and medians of variables of 32 nests of Black Oystercatchers and their matched points in the Gulf Islands, 1987

Variables	Nest sites		Matched points		Significance		
	Mean ± SD	Median	Mean ± SD	Median	χ^2	df	P
Distance (cm) to nearest log or rock ≥ 10 cm high	0.14 ± 0.16	0.10	0.65 ± 0.60	0.252	16.53	1	0.000
Microslope (°)	11.8 ± 3.9	11.0	22 ± 17	15.5	5.28	1	0.022

Table 4
Predominant material and colour of 32 nests of Black Oystercatchers in the Gulf Islands, 1987

Nest material	%	Nest colour	%
Rock chips	65.6	Grey	56.3
Shells, bones	31.3	White	31.2
Wood chips	3.1	Brown	12.5

In the 1960s, nesting Glaucous-winged Gulls in the Gulf Islands were mostly restricted to the vegetated parts of islands (Vermeer and Devito, this publication). During the present survey, we observed that gulls had invaded the bare rocky island perimeters, where oystercatchers nest. The recent gull invasion into traditional oystercatcher habitat may force oystercatchers to nest nearer to the shoreline, where the nests may be more subject to storms. We observed that oystercatchers in gull colonies nested on average 5.38 ± 2.41 m (n = 13) from the barnacle zone, whereas those on islands without gulls nested on average 8.24 ± 5.07 m (n = 19) from that zone. Hartwick (1974) suggested that, on Cleland Island, oystercatchers nesting in higher areas near land vegetation are more vulnerable to gull predation, whereas those nesting close to the shoreline may escape the threat of gulls but are highly vulnerable to washout by storms. On Destruction Island, Nysewander (1977) observed that oystercatchers associated with low densities of gull nests hatched significantly more eggs than did those associated with high densities of gull nests. Because of the extensive predation by crows and gulls on oystercatchers and the gulls' recent invasion into oystercatcher habitat, it may no longer be beneficial (if it was before) for oystercatchers to nest in association with gulls in the Gulf Islands.

6.3. Unutilized habitat

We noted that much apparently suitable nesting habitat was not occupied by oystercatchers in the Gulf Islands. The nesting territory of oystercatchers is generally contiguous with their feeding territory (Hartwick 1976; Nysewander 1977), although the birds forage at times at distant reefs or islands (Hartwick 1978). Low oystercatcher densities could therefore reflect a lack of food. In British Columbia, foods of adult birds and chicks consist mostly of mussels and limpets, but also of annelids, barnacles, chitons, crabs, isopods, oysters, sea cucumbers, and snails (Hartwick 1976; Butler and Kirbyson 1979; Groves 1982). Our subjective observations suggest that intertidal organisms, on which Black Oystercatchers feed, are relatively abundant near established gull colonies in the Gulf Islands. This relative abundance of invertebrates may result from excrement of gulls and associated nesting cormorants, which fertilizes and enriches the intertidal community near seabird colonies. Bosman and Hockey (1986) observed that the shores of seabird islands on the west coast of South Africa were characterized by significantly higher levels of nutrients than were the shores of the nearby mainland. These high nutrient levels, together with predation of African Black Oystercatchers (*Haematopus moquini*) on intertidal herbivorous limpets, led to extensive development of algal mats. Intertidal invertebrates settled on those mats and provided food for shorebirds.

7. Recommendations

We recommend that interactions between Black Oystercatchers and Glaucous-winged Gulls in the Gulf Islands be studied in detail. Reproductive success of oystercatchers and relative densities of prey organisms should be compared on islands with and without gulls. The Black Oystercatcher population in the Gulf Islands should be monitored in conjunction with that of Glaucous-winged Gulls every 5–10 yr. The nesting population of Black Oystercatchers in the Strait of Georgia outside the Gulf Islands should also be censused, as currently only incidental information exists for that population.

8. Acknowledgements

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Population, nesting habitat, and food of Bald Eagles in the Gulf Islands

Kees Vermeer, Ken H. Morgan, Robert W. Butler, and G.E. John Smith

1. Abstract

In 1987, the nesting population of Bald Eagles (*Haliaeetus leucocephalus*) in the Gulf Islands of the Strait of Georgia was surveyed, and the nesting habitat and prey of the birds were investigated. Of 120 nests observed, 81% were occupied. Nest densities averaged 0.15 nests per kilometre of shoreline. The eagle population has increased 30% over the last decade, which may reflect an increase in the eagle's main prey, the Glaucous-winged Gull (*Larus glaucescens*). Of 278 prey remains found beneath nesting trees of eagles, birds constituted 52.2%, fishes 33.5%, marine invertebrates 11.8%, and mammals 2.5%. The Glaucous-winged Gull was by far the most frequent prey species (35%). Nests of eagles with chiefly gull remains were significantly nearer to gull colonies than were nests where fish remains predominated.

Eagles nested significantly more on northeastern than on southwestern shorelines. Nesting islands were significantly larger and more frequently inhabited by people than were nonnesting islands. Nests averaged 138 ± 118 m from shore and were observed only in Douglas fir (*Pseudotsuga menziesii*) trees, at an average height of 32.4 ± 9.5 m above ground. Nesting trees were significantly taller and larger in diameter than matched trees. Nest sites of eagles had droppings of river otters (*Lutra canadensis*) and nests of Northwestern Crows (*Corvus caurinus*) associated with them.

2. Résumé

En 1987, la population nicheuse d'Aigles à tête blanche (*Haliaeetus leucocephalus*) des îles Gulf a été recensée, et l'habitat de nidification ainsi que l'alimentation des oiseaux ont été étudiés. Les nids observés, au nombre de 120, étaient occupés à 81 %. Leur densité moyenne était de 0,15 par kilomètre du littoral. Au cours de la dernière décennie, la population a augmenté de 30 %, ce qui pourrait être dû à une augmentation de la principale proie des aigles : le Goéland à ailes grises (*Larus glaucescens*). Les 278 restes de proies trouvés au bas de nids d'aigles étaient constitués à 52,2 % d'oiseaux, à 33,5 % de poissons, à 11,8 % d'invertébrés marins et à 2,5 % de mammifères. Le Goéland à ailes grises était de loin la proie la plus fréquente (35 %). Les nids d'aigles où l'on a trouvé principalement des restes de goélands se trouvaient nettement plus près de colonies de goélands que les nids où des restes de poissons prédominaient.

Les nids étaient plus nombreux sur les côtes nord-est que sur les côtes sud-ouest. Les îles où les aigles se trouvaient étaient plus grosses et plus souvent habitées. Les nids n'ont été observés que dans des Douglas taxifoliés (*Pseudotsuga menziesii*) et ils étaient situés en moyenne à 138 ± 118 m du rivage et à 32,4 ± 9,5 m du sol. Les arbres contenant un nid étaient nettement plus grands et plus gros. On a observé en association avec les nids d'aigles des excréments de Loutres de rivière (*Lutra canadensis*) et des nids de Corneilles du Nord-Ouest (*Corvus caurinus*).

3. Introduction

The nesting population of Bald Eagles (*Haliaeetus leucocephalus*) in the Gulf Islands of the Strait of Georgia was surveyed first in 1963–64 (Hancock 1964, 1965) and again in 1974 (Trenholme and Campbell 1975). The population showed little change over the 10-yr period. Trenholme and Campbell (1975) suggested that the increasing human demand for residential and recreation space on the Gulf Islands could be a major cause of loss of nesting habitat to eagles. The purposes of this study were:

(1) to assess the size of the Bald Eagle population;
(2) to determine which islands and sites Bald Eagles selected for nesting in the Gulf Islands; and
(3) to determine how important Glaucous-winged Gulls (*Larus glaucescens*) were in the present diet of Bald Eagles, as eagle visits to gull colonies have become more frequent (Vermeer and Devito, this publication).

4. Methods

4.1. Population and island habitat

The nesting population of Bald Eagles in the Gulf Islands was surveyed from a Cessna float plane on 27 March and on 9–10 April 1987 by two observers who plotted the location of all nests on 1:40 000 Canadian Hydrographic Service (CHS) charts. Each survey lasted 5.5 h. All islands in the study area (Fig. 1) were circled by plane at an altitude of about 75 m above the highest treetops. Nests were classified as either occupied or unoccupied. A nest was considered occupied if one or two adults were seen on or near the nest during one or both surveys. The fact that no eagles were seen at nests that we classified as "unoccupied" does not mean all those nests were not in use, because eagles may have been absent from nests at the time of the census. Some nests were undoubtedly missed. The census therefore represents a conservative estimate of the nesting population of Bald Eagles in the Gulf Islands (Table 1).

The areas and perimeters of all nesting and non-nesting islands were calculated from CHS charts and by planimeter.

4.2. Nest sites

For 120 nests observed from the air, the distances of nests to the nearest shoreline (high-tide line) and to the nearest gull colony (≥ 25 nesting pairs) were measured either directly or with the aid of CHS charts. In early June, an attempt was made to locate by boat most of the nests observed in March and April from the air. For 35 nests located by boat, the height of each nesting tree and nest height from the ground were measured by clinometer; the diameter at breast height (dbh) of each nesting tree was measured by tape; and the distance of each nesting tree to the nearest human dwelling was measured. In addition, a sketch of the location of each nest in its tree was made, and the surrounding forest composition and its average canopy height were noted.

In early July, the 35 nest sites were visited again to investigate nest site selection by eagles. We applied matched point analysis as used by Vermeer and Devito (1987). To select a matched point tree, we located the nearest tree or snag (to a nesting tree) with a dbh of at least 66 cm, which was the smallest diameter of the 35 nesting trees measured.

4.3. Food

We searched beneath each nesting tree for food remains dropped by eagles. We labeled, where possible, each prey organism separately and placed food remains from each nesting tree in separate plastic bags. In the laboratory, these remains were identified to the nearest possible taxon.

Figure 1
(A) Distribution of nest sites of Bald Eagles in the Gulf Islands. (B) Distribution of eagle nests in relation to orientation of shorelines. Numbered nest sites are identified in Table 1.

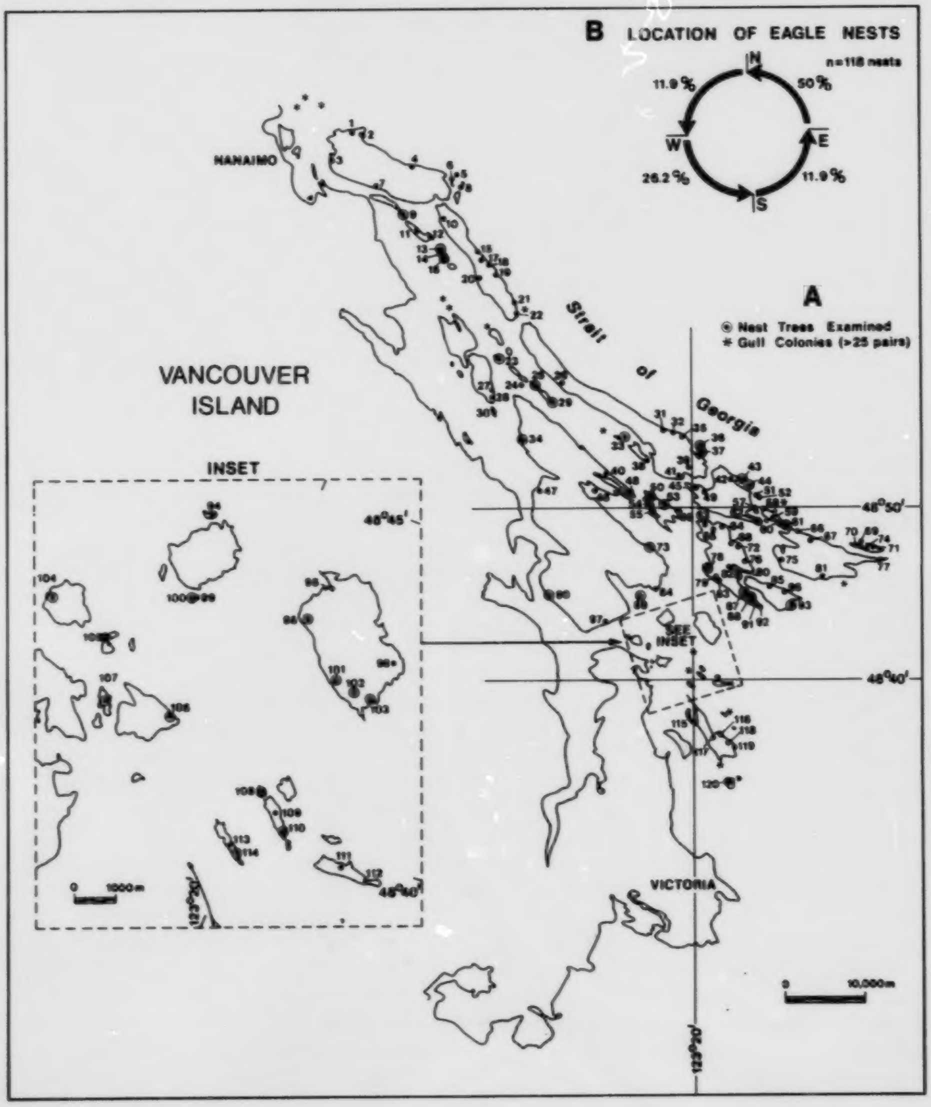

B
LOCATION OF EAGLE NESTS
n=118 nests
N
E
S
W
11.9 %
50 %
11.9 %
26.2 %
A
⊙ Nest Trees Examined
* Gull Colonies (>25 pairs)
NANAIMO
Strait of Georgia
VANCOUVER ISLAND
INSET
SEE INSET
48°50'
48°40'
48°45'
48°40'
0 1000m
0 10,000m
123°20'
123°20'
VICTORIA

Table 1
Location of nests of Bald Eagles observed from an airplane in the Gulf Islands on 27 March and 9–10 April 1987

Island name and nest location	Occupied	Unoccupied	Island name and nest location	Occupied	Unoccupied
1. Gabriola	×		61. Samuel*	×	
2. Gabriola	×		62. Mayne	×	
3. Gabriola	×		63. North Pender	×	
4. Gabriola	×		64. North Pender		×
5. Gaviola		×	65. North Pender	×	
6. Vance	×		66. Saturna	×	
7. Gabriola	×		67. Saturna	×	
8. Saturina	×		68. North Pender	×	
9. Link**	×		69. Cabbage	×	
10. Valdes		×	70. Tumbo	×	
11. DeCourcy	×		71. Tumbo		×
12. DeCourcy	×		72. North Pender	×	
13. Ruxton*	×		73. Saltspring*	×	
14. Ruxton		×	74. Tumbo	×	
15. Valdes		×	75. Saturna	×	
16. Ruxton*	×		76. North Pender	×	
17. Valdes	×		77. Saturna	×	
18. Valdes	×		78. North Pender*	×	
19. Valdes	×		79. North Pender		×
20. Valdes	×		80. North Pender		×
21. Valdes	×		81. Saturna	×	
22. Valdes	×		82. North Pender	×	
23. Norway*	×		83. North Pender	×	
24. Jackscrew	×		84. Saltspring	×	
25. Wallace*	×		85. South Pender	×	
26. Galiano	×		86. South Pender		×
27. Kuper	×		87. North Pender*	×	
28. Kuper	×		88. North Pender*	×	
29. Wallace*	×		89. Russell*	×	
30. Tent	×		90. Saltspring*	×	
31. Galiano	×		91. North Pender		×
32. Galiano	×		92. North Pender	×	
33. Charles*		×	93. South Pender*	×	
34. Saltspring*		×	94. Chads	×	
35. Galiano	×		95. Moresby*	×	
36. Gossip*	×		96. Moresby*	×	
37. Gossip*	×		97. Saltspring	×	
38. Parker	×		98. Moresby	×	
39. Galiano		×	99. Hood		×
40. Saltspring	×		100. Hood*	×	
41. Galiano	×		101. Moresby*	×	
42. Mayne	×		102. Moresby*	×	
43. Mayne*	×		103. Moresby*	×	
44. Mayne*	×		104. Piers*	×	
45. Mayne	×		105. Knapp*	×	
46. Goat		×	106. Coal*	×	
47. Saltspring	×		107. Goudge*	×	
48. Saltspring	×		108. Unnamed*	×	
49. Mayne		×	109. Domville	×	
50. Prevost*	×		110. Domville*	×	
51. Georgeson	×		111. Gooch	×	
52. Georgeson		×	112. Gooch	×	
53. Prevost*	×		113. Forrest	×	
54. Prevost	×		114. Forrest*		×
55. Prevost	×		115. Sidney (Lagoon)		×
56. Prevost		×	116. Sidney	×	
57. Curlew		×	117. Sidney	×	
58. Samuel	×		118. Sidney		×
59. Samuel	×		119. Sidney	×	
60. Samuel	×		120. D'Arcy		×
Total				**97**	**23**

* Asterisk indicates the nesting trees that were measured in June 1987.

4.4. Statistical analysis

The statistical analyses presented here compare nesting with nonnesting islands (Table 2) and nesting trees to matched point nonnesting trees (Table 3). The distribution of the data that are summarized in these tables is highly skewed, with nonhomogeneous variances. Therefore, comparisons of means could not be carried out using the classical two-sample *t*-tests or *F*-tests, or even by means of some nonparametric tests; instead, inferences about equality of the medians and the distributions were made using two-way chi-square contingency tables. However, the means and standard deviations are presented for descriptive purposes. Only forested islands were considered, as no eagles nested on nonforested islands in our study area.

For each variable in Table 2, the islands were divided into two groups with approximately the same number of islands in each. Then, a two-way contingency table was constructed to test for significant differences. The data in Table 3 are paired by tree (nesting tree vs. matched tree). Differences were calculated, and a sign test determined whether the number of positive differences was significantly different from the number of negative ones.

5. Results

5.1. Population and island habitat

During the aerial surveys of the Gulf Islands, we counted 293 adult and 59 immature Bald Eagles on 27 March, and 504 adults and 121 immatures on 9–10 April. We observed 120 nests of Bald Eagles, of which 81% were occupied (Fig. 1A, Table 1). The 120 nests were found along 761.5 km of forested shoreline, and along a total of 796.2 km of forested and nonforested shoreline, indicating 0.16 nests per kilometre of forested and 0.15 nests per kilometre of total shoreline. Of 106 forested islands, 43 were used by Bald Eagles for nesting. Nesting islands were significantly larger and were more frequently inhabited by people than were nonnesting islands (Table 2).

5.2. Nest sites

Significantly more nests were observed on the northeastern than on the southwestern shores of the Gulf Islands (Fig. 1B; $\chi^2 = 8.1$, $P = 0.004$). Most of the 120 nests (83%) were found within 200 m of shore (Fig. 2). The average nesting distance from shore was 138 ± 118 m.

Of the 35 nests checked from the ground, all were found in Douglas fir (*Pseudotsuga menziesii*). Douglas firs were the tallest trees in the Douglas fir – western red cedar (*Thuja plicata*) – arbutus (*Arbutus menziesii*) forest in which eagles nested. Slightly more nests were located in treetops (57.2%) than on branches (42.8%). When located in a treetop, the nest was found either at the top or bottom end of a dead snag or in a forked branch of a live top (Fig. 3A). Nests built some distance below the top were supported by a branch or by the tree trunk (Fig. 3B). On average, nests were situated 32.4 ± 9.5 m above the ground and 6.2 ± 4.5 m below the tip of the treetop.

Comparison of nesting and matched trees showed that nesting trees were significantly larger in diameter and taller than matched trees. There were no significant differences between nesting and matched trees with respect to the distance to human dwellings (Table 3). Of the 35 nesting trees measured, 13 had droppings of river otters (*Lutra canadensis*) beneath them; 12 had nests of Northwestern Crows (*Corvus caurinus*) within a 10-m radius of the nesting tree.

5.3. Prey

Prey remains beneath nest sites probably reflect food taken by Bald Eagles throughout the year, as few fresh prey items were observed. Of 278 prey organisms found, birds made up 52.2%, fishes 33.5%, marine invertebrates 11.8%, and mammals 2.5% (Table 4). Glaucous-winged Gulls were by far the most frequent species (34.2%) of prey. Nests of eagles in which predominantly Glaucous-winged Gull remains were found were an average of 4.4 ± 2.8 km from the nearest gull colony, whereas nests where mostly fish remains were seen were an average of

Figure 2
Distance of Bald Eagle nests from shore in the Gulf Islands

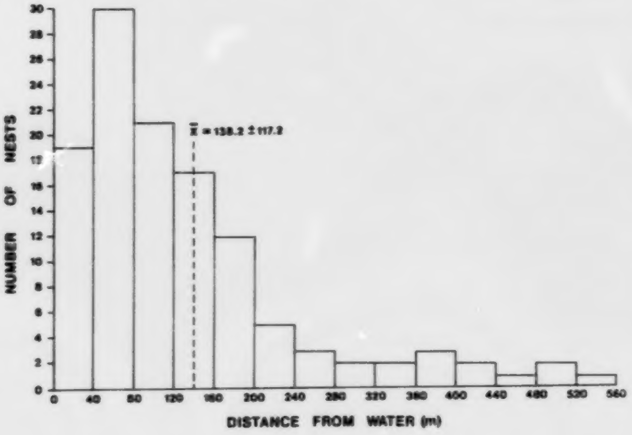


Table 2
Comparison of variables of forested islands with ($n = 43$) and without ($n = 69$) nests of Bald Eagles in the Gulf Islands

	Nesting islands			Nonnesting islands			Significance		
Variables	Mean ± SD	Median	%	Mean ± SD	Median	%	χ^2	df	P
Island area (ha)	861 ± 1878	42		37 ± 137	3		25.5	1	0.000
Island perimeter (m)	14 740 ± 25 122	4050		1890 ± 3377	845		31.3	1	0.000
Bare ground (%)	14.2 ± 22.2	10		16.4 ± 11.2	10		1.56	1	0.21
Inhabited by people			74.4			50.7	5.24	1	0.02

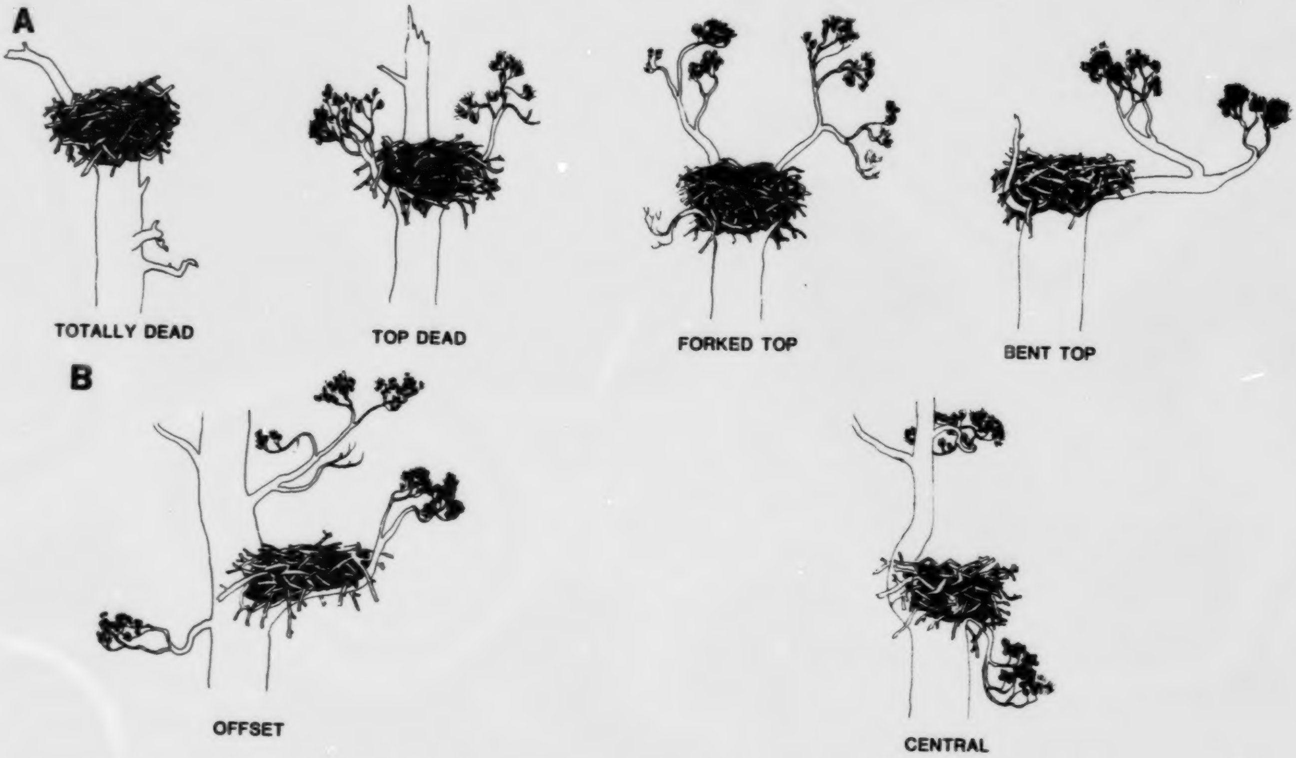
Table 3
Comparison of variables for 35 nests of Bald Eagles in trees and their matched nests in the Gulf Islands, 1987

	Nesting trees			Matched trees			Significance (Sign test)		
Variables	Mean ± SD	Median	%	Mean ± SD	Median	%	N[a]	M[b]	P
Diameter (cm)	110.0 ± 25.2	104.4		90.0 ± 19.8	85.5		35	29	0.000
Tree height (m)	38.6 ± 10.8	39.0		28.8 ± 9.8	28.5		34	28	0.000
Distance from human dwelling (m)	692 ± 806	521		694 ± 807	330		35	15	0.52
Nesting treetop above forest canopy			51.4			42.9	17	10	0.63

[a] N = number of sites at which the measurements for the nesting and matched trees are different.

[b] M = number of sites at which the measurement for the nesting tree exceeds that for the matched tree.

Figure 3
Examples of the location of Bald Eagle nests in trees:
(A) treetop nests; (B) branch nests



7.4 ± 2.7 km from the nearest gull colony. These differences were significant ($t = 2.76$, $P = 0.01$) and suggest opportunistic foraging by eagles.

6. Discussion

6.1. Population and island habitat

We observed 97 occupied and 23 unoccupied nests of Bald Eagles in the Gulf Islands, compared with 45 occupied nests and 23 locations where nesting was suspected in 1974 (Trenholme and Campbell 1975) and with 58 and 65 active nests in 1963 and 1964, respectively (Hancock 1964, 1965). The number of nests in the Gulf Islands changed little between 1963–64 and 1974 (Trenholme and Campbell 1975) but apparently increased by about 30% between 1974 and 1987. We also observed 293 adult eagles in the Gulf Islands on 27 March 1987, compared with 143 adult eagles observed by Trenholme and Campbell (1975) on 27 March 1974.

In the San Juan Islands in Washington State, immediately south of the Gulf Islands, Grubb *et al.* (1975) observed 103 nests (49 occupied and 54 unoccupied) of Bald Eagles in 1975. McAllister *et al.* (1986) surveyed the same San Juan population of Bald Eagles in 1981–85 and reported increases over estimates by Grubb *et al.* (1975). Because McAllister *et al.* (1986) provided only overall increases for Washington State, the rate of increase for the San Juan Islands cannot be compared with our findings. The nesting population of Bald Eagles in the San Juan Islands appears to be the densest in Washington State (Grubb *et al.* 1975; McAllister *et al.* 1986), whereas the total nesting population of eagles in Washington State ranks among the largest in the contiguous 48 states of the United States (Grubb *et al.* 1975). The combined Gulf and San Juan islands, therefore, constitute a very important nesting area for the species in North America.

That Bald Eagles nest on the larger islands in the Gulf Islands is not surprising. The larger islands are all forested, and the forests provide potential nest sites for eagles. The correlation between human habitation and eagle nest sites probably has no causal relationship; large islands with forests are preferred by both eagles and humans. The present substantial increase of the Bald Eagle population suggests that eagles generally have not been negatively affected by the considerable increase in numbers of human residences on the Gulf Islands that has occurred over the last decade. Most landowners we contacted were proud to have nesting eagles on their properties. The privatization of forested land may also be beneficial, in that it protects to some degree the eagles' nesting habitat from logging (Morgan *et al.* 1985). This is not to say, however, that further shoreline development and increased human activity in the Gulf Islands would not affect the nesting distribution of eagles. Fraser *et al.* (1985) observed that nests of Bald Eagles built on developed shoreline in Minnesota were significantly farther from water than those built on undeveloped shoreline. This fact suggests that eagles avoid human settlements when building new nests. Thelander (1973) reported that Bald Eagles in California avoided development when building new nests.

6.2. Nest sites

It is not surprising that most eagles in the Gulf Islands nest on northeastern and southwestern shores (Fig. 1B); there is comparatively little shoreline to the southeast and northwest because of the orientation of the

Table 4
Occurrence of prey remains ($n = 278$) found beneath 35 nest sites of Bald Eagles in the Gulf Islands

Prey category	No. of prey organisms (%)
Birds	
Glaucous-winged Gull (*Larus glaucescens*)	
— adults	80
— juveniles	6
— chicks	9
Mew Gull (*Larus canus*)	1
Pigeon Guillemot (*Cepphus columba*)	2
Cormorant (*Phalacrocorax* sp.)	4
Total seabirds	**102**
Western Grebe (*Aechmophorus occidentalis*)	2
Mallard (*Anas platyrhynchos*)	1
Green-winged Teal (*Anas carolinensis*)	1
Bufflehead (*Bucephala albeola*)	1
Goldeneye (*Bucephala* sp.)	1
Oldsquaw (*Clangula hyemalis*)	1
White-winged Scoter (*Melanitta fusca*)	1
Unidentified ducks	2
Great Blue Heron (*Ardea herodias*)	2
Northwestern Crow (*Corvus caurinus*)	2
Total grebes, ducks, and shoreline birds	**14**
Pileated Woodpecker (*Dryocopus pileatus*)	1
Unidentified woodpecker (*Picidae*)	1
Unidentified raptor	1
Unidentified gallinaceous bird	1
Unidentified other birds	25
Overall bird total	**145 (52.2)**
Mammals	
Black-tailed deer (*Odocoileus hemionus*)	1
Raccoon (*Procyon lotor*)	1
Long-tailed weasel (*Mustela frenata*)	1
Domestic sheep (*Ovis* sp.)	1
Unidentified mammals	3
Total mammals	**7 (2.5)**
Fishes	
Lingcod (*Ophiodon elongatus*)	27
Rockfishes (*Sebastes* sp.)	23
Pacific hake (*Merluccius productus*)	2
Codfishes (Gadidae)	3
Great sculpin (*Myoxocephalus polycanthocephalus*)	3
Buffalo sculpin (*Enophrys bison*)	3
Sculpins (Cottidae)	4
Flounders (Pleuronectidae)	2
Skates (Rajidae)	1
Ratfish (*Hydrolagus colliei*)	1
Salmon (*Oncorhynchus* sp.)	2
Unidentified fishes	22
Total fishes	**93 (33.5)**
Marine invertebrates	
Abalone	1
Heart cockle (*Clinocardium nuttallii*)	1
Soft-shelled clam (*Mya arenaria*)	1
Littleneck clam (*Protothaca staminea*)	4
Japanese littleneck clam (*Venerupis japonica*)	1
Butter clam (*Saxidomus giganteus*)	1
Unidentified bivalves	2
Total bivalves	**10**
Red crab (*Cancer productus*)	11
Dungeness crab (*Cancer magister*)	6
Crab (*Cancer* sp.)	1
Helmet crab (*Telmessus cheiragonus*)	1
Kelp crab (*Pugettia producta*)	1
Total crabs	**20**
Giant barnacle (*Balanus nubilus*)	1
Barnacles (*Balanus* sp.)	1
Total barnacles	**2**
Total invertebrates	**33 (11.8)**

islands in that direction (Fig. 1A). The important aspect is that eagles nested significantly more on northeastern than on southwestern shores. The reason for this preference is unknown but may relate to prevailing wind patterns. Westerly winds prevail in the Gulf Islands region at the start of the eagles' nesting season from March through May (weather information, Victoria International Airport). In strong westerlies, it may be more difficult for eagles to land and/or take off from southwestern than northeastern shores. Gerrard *et al.* (1975) observed that in anything stronger than a light wind, eagles face into the wind when landing on their nests.

The close nesting of eagles to the shoreline undoubtedly relates to their feeding activities, which primarily take place along island shores and over the water. In the diets of Bald Eagles, terrestrial prey (mammals and land birds) forms a component small compared with that of shoreline and aquatic prey (water birds, fishes, and invertebrates). Studies in Manitoba and Saskatchewan also indicate that Bald Eagles nest mostly within 180 m of rivers and lakes and prefer shoreline habitat (Whitfield *et al.* 1974; Gerrard *et al.* 1975). This preference apparently stems from the proximity of feeding opportunities (e.g., river rapids and spawning areas of fish) (Gerrard *et al.* 1975; Barber *et al.* 1983). The reason that Bald Eagles nest in the tallest trees in the Gulf Islands may relate both to visibility and to ease of landing and takeoff. Besides nesting in tall trees, eagles frequently perched in treetops not far from the nest, which provided a good view of adjacent shores and water. The nest location also relates to support structure, as a tall tree without strong branches obviously does not offer good nesting prospects.

The association of otter droppings and crow nests with eagle nest sites presumably relates to prevalence of prey remains that eagles discard. Otter droppings, which consisted mostly of further digested fish and bird remains, were found either directly beneath the nesting tree or along a trail (apparently made by the otter) leading to the tree. Nest sites of eagles remain in the same location for many years and may become important feeding stations for local otter populations. Crows probably nest near Bald Eagle nests for the same reason. Several eagle nest sites that we visited were preempted by scavenging otters before we arrived. Fielder (1982) reported that coyotes (*Canus latrans*) and raccoons (*Procyon lotor*) competed with researchers for prey remains dropped under perches of Bald Eagles wintering on the Columbia River in Washington.

6.3. Prey

Bald Eagles feed on both dead and live fishes. Bald Eagles have been observed feeding upon Pacific hake (*Merluccius productus*) at a tidal upwelling site at Active Pass, between Mayne and Galiano islands (KV, pers. obs.); one of the nest sites on Mayne Island contained remains of hake. The Pacific hake is a benthic fish that in spring can be rapidly brought to the surface by the process of upwelling in Active Pass. Such fish apparently die in the process by gas embolism. Swim bladders were observed protruding through the mouths of dying hake, which popped to the surface. Bald Eagles feed upon these hake by seizing the fish with their talons at the water surface. Eagles anticipate the appearance of the prey at the upwelling site, as up to 50 eagles were observed to line up in trees along Active Pass, 1–2 h in advance of the appearance of hake. Many of the benthic fish remains beneath nest sites may have also been obtained by eagles from fish discarded by fishermen, as we observed mostly fish heads and parts of the pectoral girdle but relatively few pelvic fin or tail bones. Many of the nonbenthic fish may have been caught alive by eagles. One of us (KHM) observed an eagle take a live rockfish from the water surface. Fishermen have informed us that they have observed eagles catching live salmon. Retfalvi (1970) observed eagles catching live fish near San Juan Island. As in our study, the fish remains found by Retfalvi (1970) were mostly those of lingcod (*Ophiodon elongatus*) and rockfish.

Eagles have on several occasions been observed to capture and kill birds. In a mixed colony of Ancient Murrelets (*Synthliboramphus antiquus*) and Cassin's Auklets (*Ptychoramphus aleuticus*) in the Queen Charlotte Islands, the main prey of Bald Eagles were adult Ancient Murrelets (Vermeer *et al.* 1984), which were killed by eagles when they arrived at their nesting burrows beneath the tree canopy at night. Fielder (1982) reported that American Coots (*Fulica americana*) were the most important food items of wintering Bald Eagles along Lake Pateros near the Columbia River in Washington. Bald Eagles captured individual coots by separating them from a flock and forcing them to dive repeatedly until fatigued. Sherrod *et al.* (1976) observed that Bald Eagles preyed upon ptarmigan (*Lagopus* spp.) in Alaska by flying low, rising over the tundra mounds and surprising their prey. Similar behaviour by a Bald Eagle was observed in the capturing and killing of a Glaucous-winged Gull on its nest in the Gulf Islands (Vermeer and Devito, this publication). Munro (1923) observed a Bald Eagle capturing a Glaucous-winged Gull in flight. The eagle followed every turn the gull made and finally grasped the prey with its talons. One of us (KHM) observed an eagle chasing for about 5 min, and thereby exhausting, an adult Glaucous-winged Gull, which finally landed on the water; there the eagle captured the gull and later ate it on the beach. R. Thomson (pers. commun.) observed two eagles chasing a Glaucous-winged Gull for 40 min, after which the exhausted gull landed on the beach, where the eagles pounced upon the gull and killed it. Bald Eagles have also been observed capturing chicks of Mew Gulls (*Larus canus*) on the water with their talons (Vermeer and Devito 1986). Besides capturing and killing birds, Bald Eagles pirate food from other birds (Fischer 1985; Frenzel 1985; Bayer 1987) or feed upon dead ones (Frenzel 1985).

Birds often predominate in the diet of eagles in the marine environment—e.g., in Alaska (Murie 1940; Sherrod *et al.* 1976) and in Maine (Todd *et al.* 1982). At certain inland localities, eagles eat chiefly benthic fishes—e.g., in Ohio (Herrick 1924), in New Brunswick (Wright 1953), in Minnesota (Dunstan and Harper 1975), in Florida (McEwan and Hirth 1980), and in Maine (Todd *et al.* 1982). Todd *et al.* (1982) observed that 11 species of seabirds and 12 species of waterfowl comprised 67% of the food remains of eagles in coastal Maine. *Larus* gulls (mostly Herring Gull [*L. argentatus*] and Great Black-backed Gull [*L. marinus*]) made up 24% of all food items of eagles in Maine; this approaches the extent of eagle predation on gulls we observed in the Gulf Islands (35%).

Most of the mammalian remains we found beneath nest sites of eagles in the Gulf Islands may have been acquired as carrion. Retfalvi (1970) reported that, on San Juan Island, nesting eagles fed mostly on domestic rabbits, which were chiefly picked up as road kills and as victims of hay cutting machines. He also observed eagles feeding on a beached harbour seal (*Phoca vitulina*).

With respect to intertidal foraging, eagles have been observed feeding on intertidal invertebrates on the BC coast on five occasions (KV, pers. obs.). Hawbecker (1958) reported a Bald Eagle eating many abalones. Retfalvi (1970) observed an eagle taking a crab from the beach to its nest.

6.4. Eagle–gull interactions

The Glaucous-winged Gull population in the Strait of Georgia and the Gulf Islands has doubled since 1960, and Bald Eagles visit gull colonies now much more frequently (Vermeer and Devito, this publication). The increasing eagle population in the Gulf Islands may therefore reflect an increase in the population of their main prey, the Glaucous-winged Gull, as well as a greater utilization of that prey. The Bald Eagle is also responsible for much of the reproductive failure of small gull colonies in the Gulf Islands (Vermeer and Devito, this publication). Glaucous-winged Gulls now appear to negatively affect nesting American Black Oystercatchers (*Haematopus bachmani*) in the Gulf Islands (Vermeer, Morgan, and Smith, this publication) and are becoming a nuisance in cities in the region (Vermeer *et al.* 1988). However, present eagle predation on gulls may curb some of the gull increase and its consequences.

7. Recommendations

We recommend that the Bald Eagle and Glaucous-winged Gull populations in the Gulf Islands be censused simultaneously every 10 yr. That census should preferably be conducted in cooperation with one in the San Juan Islands, as these islands are part of the same island chain. This chain harbours an important component of the North American Bald Eagle population. We also recommend that nesting Bald Eagles be surveyed in the northern end of the Strait of Georgia, as we know little about that population. The interactions between Bald Eagles and Glaucous-winged Gulls in gull colonies should be studied in detail, as at present there is mainly only qualitative information on the subject.

8. Acknowledgements

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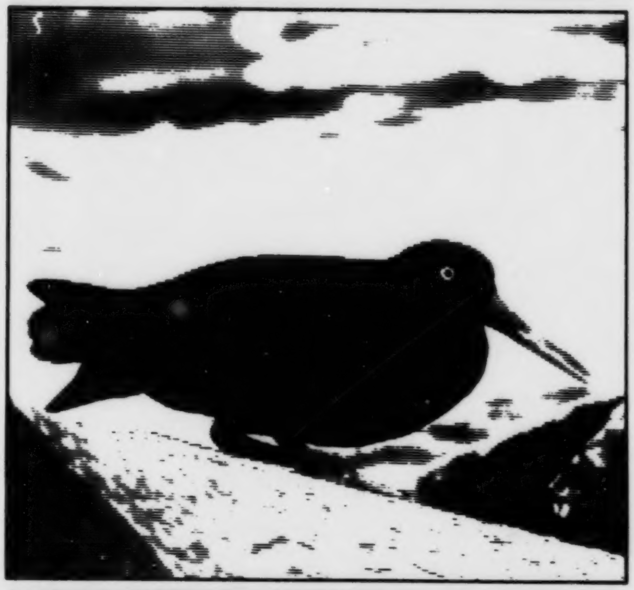
Part 5

Populations and ecology of wintering birds



Birds of rocky coastlines and pelagic waters in the Strait of Georgia

Jean-Pierre L. Savard

1. Abstract

The rocky shores and pelagic waters of the Strait of Georgia in British Columbia support a great diversity of birds. Four species of waterfowl and four species of shorebirds occur mostly along rocky shores: Barrow's Goldeneye (*Bucephala islandica*), Surf Scoter (*Melanitta perspicillata*), Black Scoter (*M. nigra*), Harlequin Duck (*Histrionicus histrionicus*), American Black Oystercatcher (*Haematopus bachmani*), Black Turnstone (*Arenaria melanocephala*), Surfbird (*Aphriza virgata*), and Rock Sandpiper (*Calidris ptilocnemis*). The level of knowledge about wintering ecology and habitat preference varies between species but is generally poor. The pelagic waters of the Strait of Georgia do not support an abundance of pelagic birds, and little is known of the ecology and behaviour of the species that frequent those offshore waters. Greater understanding of these coastal and marine ecosystems is needed before a proper management approach for these species can be developed.

2. Résumé

Les rivages rocheux et les eaux pélagiques du détroit de Georgia en Colombie-Britannique font vivre une grande variété d'oiseaux. Quatre espèces de gibiers d'eau (sauvagine) et quatre espèces d'oiseaux de rivage sont observées principalement sur les rivages rocheux : le Garrot de Barrow (*Bucephala islandica*), la Macreuse à front blanc (*Melanitta perspicillata*), la Macreuse à bec jaune (*M. nigra*), le Canard arlequin (*Histrionicus histrionicus*), l'Huîtrier noir (*Haematopus bachmani*), le Tournepierre noir (*Arenaria melanocephala*), le Bécasseau du ressac (*Aphriza virgata*) et le Bécasseau des Aléoutiennes (*Calidris ptilocnemis*). Les connaissances sur les caractéristiques écologiques hivernales et les préférences pour l'habitat varient d'une espèce à l'autre, mais elles sont généralement faibles. Les eaux pélagiques du détroit n'accueillent pas un grand nombre d'oiseaux pélagiques, et on sait peu de chose sur les caractéristiques écologiques et le comportement des espèces qui fréquentent ces eaux. On devra obtenir plus de connaissances sur les écosystèmes côtiers et marins de la région pour pouvoir élaborer une approche adéquate pour la gestion de ces espèces.

3. Introduction

The Strait of Georgia in British Columbia supports a great diversity of aquatic birds in all seasons, but especially in winter, when sea ducks predominate among the avifauna (Vermeer *et al.* 1983). Within the Strait of Georgia, most rocky foreshores are located in remote and inaccessible areas; therefore, information on bird use of such habitats is scarce. This is especially true for the shorebirds that often frequent offshore rocky islands.

Rocky shores are characterized by the predominance of sessile organisms vertically distributed on the rock surface according to their resistance to desiccation, wave action, and the intensity of interspecific competition and predation (Boaden and Seed 1985). These sessile organisms provide refugia against predation and desiccation for a great diversity of other invertebrates, which in turn provide food for several species of birds. Rocky shorelines are highly variable in type, ranging from steep cliffs to gently sloping platforms, with smooth to highly dissected beaches (Lewis 1977), and all types are found within the Strait of Georgia.

Characterization of the bird species associated with rocky coastlines is difficult because there have been few studies on habitat use by water birds in coastal areas or on the classification of the rocky coastal habitat types that water birds use. A few studies have shown that the Harlequin Duck (*Histrionicus histrionicus*) and Barrow's Goldeneye (*Bucephala islandica*) are found almost exclusively along rocky shores (Mitchell 1952; Vermeer 1982, 1983*a*; Goudie 1984; Dzinbal and Jarvis 1984). However, those species are rarely found together, as they prefer very different types of rocky shores. Harlequin Ducks feed mostly on molluscs and crustaceans associated with macroalgae along rocky shores (Vermeer 1983*a*; Dzinbal and Jarvis 1984; Goudie 1984), and Barrow's Goldeneyes eat mostly blue mussels (*Mytilus edulis*) (Vermeer 1982; Koehl *et al.* 1984) attached to exposed rocky substrates.

The offshore waters of the Strait of Georgia are greatly influenced by the discharge of the Fraser River and thus differ from the waters off the west coast of Vancouver Island (Thomson 1981). The waters of the strait are relatively productive (Parsons *et al.* 1969, 1970), but preliminary surveys indicate that they do not support large numbers of pelagic birds (Robertson 1977).

Several studies have documented the distribution and abundance of sea ducks within various sections of the Strait of Georgia (Mitchell 1952; Vermeer *et al.* 1983; Vermeer 1983*b*). Hirsch (1980) studied the ecology of sea ducks frequenting nearby Puget Sound in Washington. In this paper, I review what is known about the abundance and distribution of birds frequenting the open rocky shore and the offshore waters of the Strait of Georgia and identify research needs.

4. Methods

Ground counts were conducted along two types of rocky shores to determine the species of waterfowl frequenting these habitats. Five kilometres of shoreline were surveyed around Stanley Park in Vancouver. The foreshore is characterized by a mixture of rocky platforms and rocky outcrops separated by sandy and boulder beaches. These rocky areas support dense populations of blue mussels. Four kilometres of shoreline were surveyed between White Rock and Crescent Beach, about 30 km south of Vancouver. The foreshore there is characterized by the absence of rocky platforms and outcrops; rather, it is a mixture of gravel, sand, and cobbles, with a few large rocks supporting some mussels. Observations on Barrow's Goldeneye and Surf Scoters (*Melanitta perspicillata*) were made mainly near Stanley Park, whereas those on Harlequin Ducks were made mostly near White Rock. During surveys, all birds within 200 m of shore were counted, and observations were recorded on cassette tape.

Most of the information on the distribution and relative abundance of birds within the Strait of Georgia was compiled from the results of the 10 Christmas Bird Counts done within the strait (Fig. 1). Unless otherwise indicated, sex ratios are biased toward females, as usually immature males could not be separated from females.

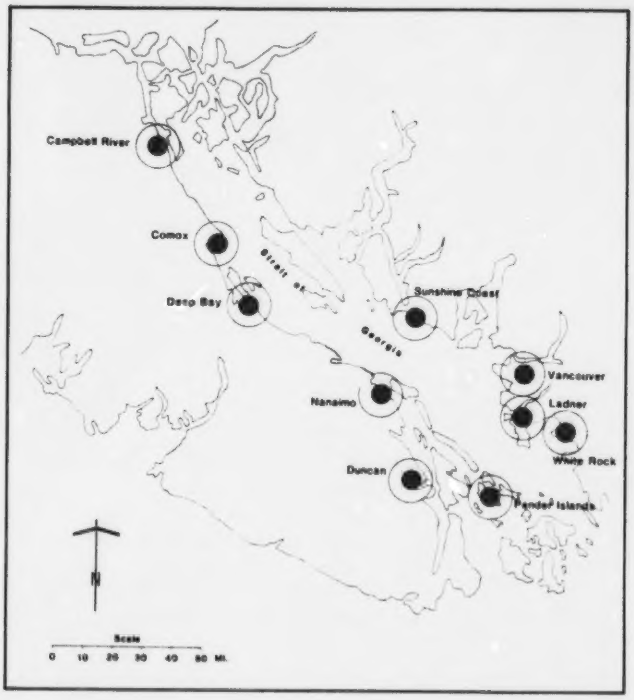
5. Results and discussion

The wintering distribution of diving ducks within the Strait of Georgia (based on the results of the 10 Christmas Bird Counts) suggests different habitat preferences among the species (Table 1, Fig. 1). The abundance of each species (based on the mean of eight counts) varies between areas, and measures of association between species indicate few strong associations (Table 2).

The abundance of Black Scoters (*Melanitta nigra*) was significantly correlated with the presence of Harlequin Ducks and indicated that they may prefer similar habitats. Birds that were significantly correlated with Barrow's Goldeneye included the Surf Scoter (0.93, Pearson's coefficient), Lesser Scaup (*Aythya affinis*; 0.79), Red-breasted Merganser (*Mergus serrator*; 0.75), and Common Goldeneye (*Bucephala clangula*; 0.73). Of those, however, none was significantly correlated based on rank correlation, which raises doubts about the ecological significance of the parametric correlation, considering the small sample sizes involved.

A survey of a 5-km-long rocky shore in Stanley Park, Vancouver, shows the predominance of two species in that habitat: the Barrow's Goldeneye and the Surf Scoter (Table 3). A similar survey near White Rock along a 4-km-long rocky and sandy shore frequented by Harlequin Ducks revealed a more diversified aggregate of species (Table 4). The most abundant species were the Surf Scoter and Black Scoter, followed by smaller numbers of the White-winged Scoter (*Melanitta fusca*), Common Goldeneye, and Harlequin Duck. Comparisons based on relative abundances are, however, somewhat misleading, because of differences in total population of these species along the coast. Surf Scoters are much more abundant than Harlequin Ducks along the coast of British Columbia (Vermeer *et al.* 1983).

Figure 1
Map of Christmas Bird Count locations



5.1. Seasonal abundance and distribution of four species of diving ducks

Eight species of sea ducks winter in the Strait of Georgia in large numbers (Table 1). Of these, four species feed on organisms found mainly over rocky substrates and frequent rocky shores: the Surf Scoter, Barrow's Goldeneye, Black Scoter, and Harlequin Duck (Table 5). The Oldsquaw (*Clangula hyemalis*) often frequents offshore waters and will be discussed with offshore birds.

5.1.1. Surf Scoter

Little is known about the annual cycle of Surf Scoters, because the species has never been studied on its breeding ground. Birds wintering in the Strait of Georgia probably breed mostly in Alaska, the Yukon, and the Northwest Territories (Palmer 1976). Spring observations of groups of Surf Scoters on lakes of central British Columbia (pers. obs.) indicate that some birds migrate overland to their breeding areas.

In the spring, migration starts in late March, and often birds congregate along the coast at herring spawning sites (Munro and Clemens 1931; Vermeer 1981). Din (1977) reported 663 Surf Scoters near Stanley Park on 16 March and none on 30 March, indicating that birds may have already left this wintering site. Several Surf Scoters remain in the Strait of Georgia during the summer to moult (Vermeer and Levings 1977; Savard 1988*b*). These birds are thought to be mostly subadults and nonbreeding adults. Sex ratios (male:female) taken near White Rock averaged 4.27:1 (n = 4 counts) in June and 4.23:1 (n = 10 counts) in July.

Surf Scoters concentrate in discrete moulting areas during the summer, such as Boundary Bay, Christie Islet in Howe Sound, Vargas Island, and the Comox area (Savard 1988*b*; Fig. 2). Small flocks have been reported in the Gulf Islands in summer, but no discrete moulting sites have

Table 1
Average number of diving ducks (± SE) seen between 1978 and 1985 in the 10 Christmas Bird Counts[a] conducted annually in the Strait of Georgia (n = 8)

	Vancouver Island area						Mainland coast area			
Species	Pender Island	Duncan	Nanaimo	Deep Bay	Comox	Campbell River	Sunshine Coast	Vancouver	Ladner	White Rock
Ring-necked Duck	38 ± 7	147 ± 31	39 ± 11	3 ± 2	4 ± 1	2 ± 1	0	3 ± 1	2 ± 1	2 ± 1
Canvasback	–[b]	5 ± 2	-	-	5 ± 2	1 ± 1	-	53 ± 11	128 ± 40	105 ± 24
Greater Scaup	21 ± 6	110 ± 32	46 ± 6	1359 ± 138	804 ± 113	150 ± 28	38 ± 5	2380 ± 327	1388 ± 349	2305 ± 888
Lesser Scaup	2 ± 1	531 ± 87	41 ± 10	22 ± 15	31 ± 6	11 ± 7	8 ± 3	1030 ± 277	84 ± 28	416 ± 341
Common Goldeneye	103 ± 17	245 ± 57	144 ± 12	441 ± 37	394 ± 36	184 ± 14	147 ± 20	688 ± 126	261 ± 40	172 ± 43
Barrow's Goldeneye	92 ± 22	84 ± 10	196 ± 50	54 ± 10	79 ± 11	4 ± 1	506 ± 86	2197 ± 223	20 ± 6	30 ± 7
Bufflehead	276 ± 38	428 ± 100	163 ± 21	459 ± 38	378 ± 28	294 ± 63	122 ± 17	355 ± 26	787 ± 108	248 ± 34
Oldsquaw	5 ± 2	20 ± 5	10 ± 2	39 ± 19	157 ± 25	23 ± 5	25 ± 12	69 ± 13	162 ± 50	48 ± 12
Harlequin Duck	46 ± 16	1 ± 1	43 ± 7	400 ± 73	235 ± 31	113 ± 15	44 ± 10	44 ± 4	84 ± 14	61 ± 13
White-winged Scoter	31 ± 15	459 ± 164	26 ± 5	1535 ± 122	1081 ± 92	137 ± 26	68 ± 24	88 ± 10	170 ± 35	143 ± 24
Surf Scoter	208 ± 76	307 ± 86	248 ± 48	1296 ± 126	1090 ± 94	220 ± 33	1022 ± 302	4426 ± 433	928 ± 180	834 ± 277
Black Scoter	3 ± 1	20 ± 5	30 ± 12	602 ± 87	434 ± 68	446 ± 71	120 ± 29	386 ± 40	218 ± 45	264 ± 74
Hooded Merganser	81 ± 8	29 ± 4	20 ± 5	9 ± 2	10 ± 3	16 ± 3	5 ± 2	43 ± 4	15 ± 5	13 ± 3
Common Merganser	203 ± 29	852 ± 102	90 ± 12	86 ± 7	194 ± 64	243 ± 141	44 ± 14	406 ± 51	96 ± 21	83 ± 20
Red-breasted Merganser	143 ± 42	107 ± 19	64 ± 4	49 ± 6	124 ± 23	42 ± 8	30 ± 6	268 ± 27	126 ± 16	81 ± 13
Ruddy Duck	0	54 ± 16	11 ± 2	0		0	0	254 ± 43	271 ± 102	2840 ± 1351

[a] Source: American Birds 1976–86, Vols. 29(4), 30(4), 31(4), 32(4), 33(4), 34(4), 35(4), 36(4), 37(4), 38(4), 39(4).
[b] Less than 0.5.

Table 2
Association between species of diving ducks based on correlations in their abundance in the 10 Christmas Bird Counts in the Strait of Georgia

Spearman's correlation (underlined) / Pearson's correlation	Ring-necked Duck	Canvasback	Greater Scaup	Lesser Scaup	Common Goldeneye	Barrow's Goldeneye	Bufflehead	Oldsquaw	Harlequin Duck	White-winged Scoter	Surf Scoter	Black Scoter	Hooded Merganser	Common Merganser	Red-breasted Merganser	Ruddy Duck
Ring-necked Duck		-0.15	-0.30	0.22	-0.06	0.30	0.17	-0.44	-0.38	-0.01	-0.26	-0.42	0.59	0.53	0.39	0.02
Canvasback	-0.29		0.75*[a]	0.76*	0.45	-0.22	0.43	0.66*	0.00	0.35	0.34	-0.05	-0.06	0.14	0.57	0.90*
Greater Scaup	-0.43	0.71*		0.70*	0.76*	-0.28	0.47	0.77*	0.35	0.48	0.62	0.61	-0.11	-0.04	0.32	0.66*
Lesser Scaup	0.23	0.31	0.61		0.51	-0.08	0.33	0.37	-0.35	0.25	0.37	-0.03	0.26	0.33	0.43	0.87*
Common Goldeneye	-0.20	0.11	0.64*	0.64*		-0.12	0.73*	0.78*	0.40	0.71*	0.81*	0.68*	-0.18	0.28	0.27	0.24
Barrow's Goldeneye	-0.17	0.09	0.47	0.79*	0.73*		-0.44	-0.26	-0.66*	-0.53	0.25	-0.44	0.26	0.04	0.21	0.09
Bufflehead	0.03	0.55	0.33	0.05	0.32	-0.12		0.56	0.43	0.78*	0.35	0.35	-0.02	0.41	0.38	0.20
Oldsquaw	-0.37	0.52	0.44	-0.02	0.43	0.00	0.71*		0.53	0.60	0.78*	0.61	-0.47	-0.14	0.24	0.40
Harlequin Duck	-0.39	-0.21	0.19	-0.36	0.37	-0.24	0.25	0.36		0.58	0.27	0.78*	-0.50	-0.24	-0.13	-0.27
White-winged Scoter	-0.05	-0.27	0.13	-0.21	0.41	-0.24	0.30	0.37	0.91*		0.48	0.56	-0.44	0.07	-0.01	0.12
Surf Scoter	-0.32	0.24	0.70*	0.76*	0.89*	0.93*	0.10	0.27	0.04	-0.02		0.55	-0.47	-0.19	0.12	0.19
Black Scoter	-0.58	0.04	0.51	0.03	0.62	0.14	0.25	0.43	0.79*	0.65*	0.40		-0.50	-0.12	-0.26	-0.12
Hooded Merganser	0.28	-0.14	-0.13	0.22	-0.04	0.25	-0.08	-0.35	-0.37	-0.36	0.09	-0.43		0.76*	0.65*	0.19
Common Merganser	0.84*	-0.19	-0.13	0.57	0.22	0.20	0.14	-0.19	-0.34	-0.01	0.10	-0.24	0.29		0.54	0.08
Red-breasted Merganser	0.03	0.30	0.51	0.75*	0.67*	0.75*	0.28	0.29	-0.25	-0.18	0.76*	0.01	0.56	0.37		0.48
Ruddy Duck	-0.18	0.63*	0.61	0.28	-0.14	-0.09	-0.11	0.00	-0.17	-0.19	0.01	0.03	-0.16	-0.01	-0.17	

[a] *Asterisk indicates $P < 0.05$.

been identified (Savard 1988*b*). However, no systematic surveys have been carried out to locate moulting concentrations within the Strait of Georgia, and large sections remain unsurveyed.

Postbreeding Surf Scoters return to the Strait of Georgia in late October and early November Surf Scoters were the most abundant sea ducks in the strait in winter, where between 8000 and 13 000 were counted annually on 10 Christmas Bird Counts (Table 6). They are one of the most broadly distributed waterfowl in the Strait of Georgia, being most abundant in the Vancouver area. Boat surveys in the strait and in adjacent inlets also indicate that the Surf Scoter is the most common sea duck, with greater numbers found along the mainland coast than along Vancouver Island (Mitchell 1952; Vermeer 1981; Vermeer *et al.* 1983). Sex ratios of wintering Surf Scoters are skewed toward males, averaging 2.1 adult males per bird with female-like plumage (Table 7). The sex ratio derived from the BC Wildlife Record Scheme is 3.2 males per female for wintering birds (N.K. Dawe, pers. commun.), indicating that sex ratios may vary between areas and years. Whether this variation reflects yearly production and/or habitat preferences by various age groups of scoters is unknown. From 1975 to 1985, the number of Surf Scoters recorded in Christmas Bird Counts remained fairly stable, fluctuating between 8254 and 12 869 birds, with no obvious upward or downward trend.

5.1.2. *Barrow's Goldeneye*

The majority of Barrow's Goldeneyes wintering in the Strait of Georgia breed in central British Columbia (Savard 1985*a*, 1987). Spring migration is somewhat gradual, starting in early March and continuing to mid-April. By early May, almost all Barrow's Goldeneyes have

Table 3
Relative and absolute abundance of grebes, loons, and diving ducks observed along a predominantly rocky coast (5 km long) in Stanley Park, British Columbia, in 1986

Species	30 December	26 November	Overall relative abundance (%)
Western Grebe	4	0	0.1
Horned Grebe	5	0	0.2
Common Loon	1	0	0.0
American Wigeon	14	191	6.7
Scaup	56	157	7.0
Common Goldeneye	76	67	4.7
Barrow's Goldeneye	485	518	33.0
Bufflehead	11	17	0.9
Oldsquaw	2	0	0.1
Harlequin Duck	0	3	0.1
White-winged Scoter	0	3	0.1
Surf Scoter	724	627	44.4
Common Merganser	1	0	0.0
Red-breasted Merganser	23	53	2.5

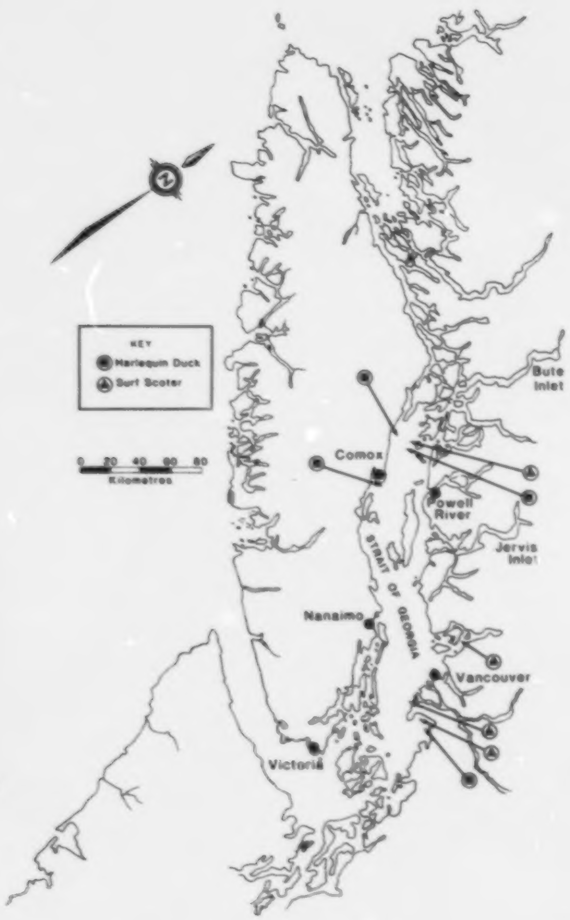
Table 4
Relative and absolute abundance of grebes, loons, and diving ducks observed along a predominantly rocky and sandy coast (4 km long) near White Rock, British Columbia (within 200 m of shore), in 1986

Species	26 November	9 December	18 December	12 January	5 February	Overall relative abundance (%)
Common Loon	9	13	14	3	6	0.8
Arctic Loon	0	0	0	9	10	0.3
Red-necked Grebe	26	15	4	2	4	0.9
Horned Grebe	95	97	75	38	35	5.8
Western Grebe	10	13	1	0	0	0.4
Common Goldeneye	84	109	77	49	58	6.5
Barrow's Goldeneye	6	4	1	12	2	0.4
Bufflehead	49	50	37	36	40	3.6
Oldsquaw	23	24	21	7	10	1.5
Harlequin Duck	70	60	74	71	68	5.9
White-winged Scoter	160	98	79	77	82	8.4
Surf Scoter	704	464	367	168	422	36.4
Black Scoter	310	380	300	222	206	24.3
Red-breasted Merganser	68	100	63	28	24	4.8

Table 5
Major prey species and foraging habitat of wintering sea ducks of the Strait of Georgia

Species	Prey species by order of importance	Foraging habitat	References
Common Goldeneye	Crustaceans, bivalves, snails, crabs	Sandy, silty, gravel, boulder-strewn substrates	Munro 1939; Vermeer and Levings 1977; Vermeer 1982
Barrow's Goldeneye	Mussels, snails, crustaceans	Exposed rocks, rocky substrates	Munro 1939; Vermeer 1982; Koehl *et al.* 1984
Bufflehead	Crustaceans, snails	Sandy, silty, gravel substrates, estuaries	Munro 1942; Erskine 1971; Vermeer 1982
Oldsquaw	Crustaceans, fishes, bivalves, snails	Subtidal waters, sandy and rocky substrates	Vermeer and Levings 1977; Hirsch 1980; Johnson 1984; Goudie 1984; Sanger and Jones 1984
Harlequin Duck	Snails, limpets, crabs, crustaceans	Algae-covered rocks, cobble beaches, kelp beds	Hirsch 1980; Vermeer 1983*a*; Fleishner 1983; Gaines and Fitzner 1987
White-winged Scoter	Bivalves, snails, crabs	Sand-mud, gravel, and cobble substrate	Stott and Olson 1972; Vermeer and Levings 1977; Sanger and Jones 1984; Vermeer and Bourne 1984
Surf Scoter	Mussels, crustaceans, other bivalves	Exposed rocks, sandy gravel substrate	Vermeer and Levings 1977; Vermeer 1981; Vermeer and Bourne 1984
Black Scoter	Mussels, snails	Sand-mud, cobble substrate, rocky shores	Vermeer and Levings 1977; Cramp and Simmons 1977; Goudie 1984; Vermeer and Bourne 1984

Figure 2
Moulting sites of Surf Scoters and Harlequin Ducks



left the coast for their breeding areas and are rare in coastal waters during the summer (Savard 1987). In late June, males leave their mates for still-unknown moulting sites (Savard 1987). To date, the only known moulting areas for male Barrow's Goldeneyes are in the Yukon and Alaska (Savard 1987).

The seasonal abundance of Barrow's Goldeneyes in the Strait of Georgia is well documented (Fig. 3). They usually first arrive in late October after breeding, and their numbers peak in mid-November. Males arrive slightly before females, which suggests that they may stage in different locations in early fall. Pairs may reunite on their coastal wintering area (Savard 1985*a*), so some pairs may be seen by early November. The number of isolated pairs increases steadily until mid-December and then remains more or less stable (Fig. 3). The sex ratio is highly biased toward males in October and November because of their earlier arrival. It then stabilizes around 1.5 males per female for the winter (Table 8).

The distribution of Barrow's Goldeneyes is clumped within the Strait of Georgia, as indicated by their abundance in the various Christmas Bird Counts (Table 1). Vancouver and the Sunshine Coast had the highest numbers. Mitchell (1952) and Vermeer (1982) also indicated the greater abundance of Barrow's Goldeneyes on the mainland coast compared with the east coast of Vancouver Island. Reasons for this pattern are unknown but could reflect relative abundance of rocky shores between the areas. Vermeer (1982) showed that Barrow's Goldeneyes and Surf Scoters were the most abundant species frequenting coastal inlets.

Barrow's Goldeneyes differ in their habitat selection according to their age and status. Paired birds often isolate themselves from wintering groups to defend exclusive territories along rocky shores (Savard 1988*a*). Groups of unpaired birds are usually found over large mussel beds, whereas pairs defend areas away from those beds (JPLS, unpubl. data). Immature (< 1 yr old) and subadult

Table 6
Population trends based on the 10 Christmas Bird Counts[a] conducted within the Strait of Georgia

Species	1975–76	1976–77	1977–78	1978–79	1979–80	1980–81	1981–82	1982–83	1983–84	1984–85	1985–86
Western Grebe	8 857	15 421	22 627	10 059	14 802	19 172	21 168	18 134	31 268	12 667	19 502
Harlequin Duck	1 125	1 119	939	927	817	1 259	1 241	1 533	895	774	1 083
Oldsquaw	653	709	665	239	609	860	524	662	735	413	448
Black Scoter	2 874	3 638	2 484	2 959	2 250	2 117	2 686	2 654	2 793	2 056	2 176
Surf Scoter	12 869	10 453	11 366	11 371	10 212	11 528	9 169	8 254	12 419	9 160	10 724
Black Turnstone	786	671	786	568	610	877	2 607	4 117	783	794	403
Surfbird	92	172	435	155	154	112	212	234	346	80	23
American Black Oystercatcher	46	93	46	32	28	52	66	63	92	76	109
Common Murre	611	792	3 651	4 828	8 433	3 631	828	3 248	2 249	778	572
Marbled Murrelet	2 385[b]	352	309	212	574	408	525	181	378	221	70
Barrow's Goldeneye	2 625	3 956	2 687	2 221	2 946	3 670	2 894	2 614	2 932	4 280	4 579
Pigeon Guillemot	54	94	29	32	52	62	35	63	73	35	74
Ancient Murrelet	112	93	86	73	0	0	0	33	15	0	0
Rock Sandpiper	12	12	12	12	52	0	3	2	482	17	16

[a] Source: American Birds 1976–86, Vols. 29(4), 30(4), 31(4), 32(4), 33(4), 34(4), 35(4), 36(4), 37(4), 38(4), 39(4).
[b] Due to an unusually high count of 2125 birds in the Ladner count.

Table 7
Sex ratios of wintering Surf Scoters near Vancouver, 1980–83

Date	No. of surveys	No. of males	No. of females	Male/female
November	5	2105	1096	1.9
December–January	8	2927	1402	2.1
February–April	4	1372	688	2.0
Total	**17**	**6404**	**3186**	**2.0**

Figure 3
Seasonal abundance of Barrow's Goldeneye in British Columbia

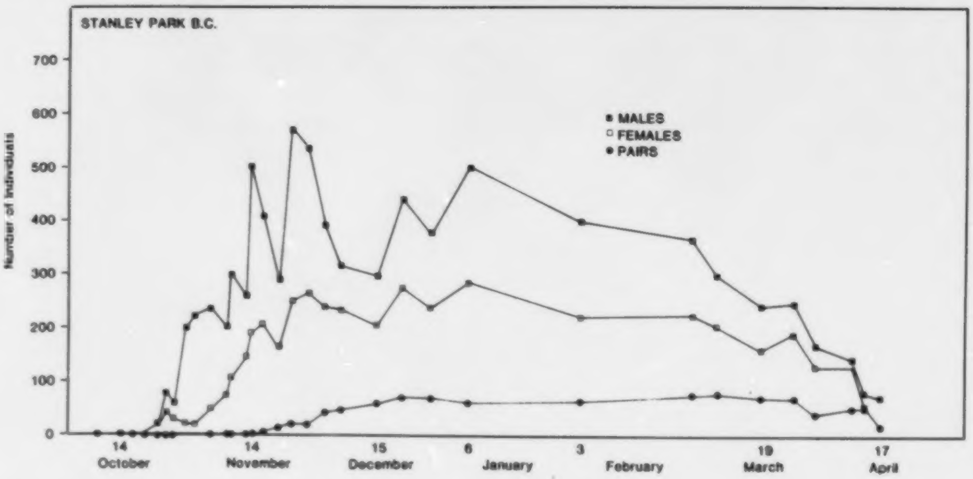


Table 8
Sex ratio of wintering Barrow's Goldeneye (counts done in Stanley Park, British Columbia, 1981–84)

Month	No. of surveys	Total no. of birds seen	Average adult sex ratio[a] (male/female) ± SE
October	5	841	4.9 ± 2.0
November	13	7127	2.4 ± 0.2
December	7	4130	1.5 ± 0.1
January–February	6	2901	1.5 ± 0.1
March	6	2670	1.5 ± 0.1
April	4	1657	1.6 ± 0.3

[a] Female category includes immature males and females, as those cannot be distinguished easily in the field.

(1–2 yr old) birds are often found with unpaired adult males and sometimes in different areas from adult birds. The abundance of immature and subadult birds varies between years and between areas along the coast (Table 9).

Philopatry to wintering areas is well developed. One pair was observed reuniting on the wintering areas in 3 consecutive years and using the same coastal territory each year (Savard 1985*a*, 1988*a*). Two other marked females were sighted in the same wintering site for 2 consecutive years. Birds from the same breeding area are dispersed along the coast. Sightings of birds marked on the breeding grounds near 100 Mile House and Riske Creek, BC, have been reported from Seattle and Vancouver. In spite of intensive surveys, only two of 200 marked females have been observed wintering near Vancouver. Recoveries of birds banded in the interior of British Columbia are scattered along the coast (Savard 1987). It is not known how the birds from a given breeding area dispersed into different wintering areas.

Winter Christmas Bird Counts of Barrow's Goldeneye fluctuated between 2221 and 4579 birds from 1975 and 1985 within the Strait of Georgia (Table 6). Counts in Puget Sound showed similar fluctuations, with a possible increase in the wintering population since 1975 (Savard 1987).

5.1.3. Black Scoter

As for Surf Scoters, little is known of the breeding ecology of Black Scoters. According to the BC Wildlife Record Scheme (R.W. Campbell, pers. commun.), spring migration starts in March, and most birds are gone by mid-May. Their migration route likely differs from that of Surf Scoters, as birds are not often sighted in central British Columbia during spring migration. In the spring, they often congregate where herring spawn (Munro and Clemens 1931). Some Black Scoters remain in the Strait of Georgia during the summer (Savard 1988*b*), but no important moulting concentration has been identified. The autumn migration begins in early September and continues through November, peaking in late October. Black Scoters are most abundant in winter, but they are the least abundant of the scoters in the Strait of Georgia (Table 1). Winter sex ratio near White Rock, BC, averaged 1.87 ± 0.22 males per female ($n = 6$ surveys) and was similar to that of Surf Scoters for the same area (1.84 ± 0.29, $n = 6$). Mitchell (1952) reported a preponderance of drakes in October (5.15 males per female), which indicates an earlier fall migration of drakes to the wintering areas. Through November this ratio became smaller and reached 0.58 males per female. However, the sex ratio was nearly even in winter (Mitchell 1952), when most birds observed were paired.

Table 9
Relative abundance of paired, male, female, immature, and subadult Barrow's Goldeneyes in various areas of the Strait of Georgia

			Composition by age and status (%)			
Area	Date	Total no. of birds seen	Isolated pairs	Adult males	Adult females	Immatures and subadults
Horseshoe Bay	22 December 1983	1774	5	37	24	34
Horseshoe Bay	29 November 1984	878	20	41	22	17
Sunshine Coast	29 November 1983	947	7	41	25	27
Stanley Park	28 January 1985	430	30	53	13	5
Okeover and Theodosia Inlet	19 February 1985	1088	30	50	15	5
Stanley Park	20 February 1985	462	25	42	24	9

Data from the BC Wildlife Record Scheme yield a male to female ratio of 1.3:1 in winter and spring (N.K. Dawe, pers. commun.). This large variation in reported sex ratios is puzzling and stresses the need for a greater understanding of the dynamics of wintering populations.

The distribution of Black Scoters was statistically correlated with that of Harlequin Ducks (Table 2). Black Scoters were most abundant in the northwest section of the Strait of Georgia between Deep Bay and Campbell River (Table 1). They rarely frequent deep inlets (Vermeer *et al.* 1983). Unlike Surf Scoters and Barrow's Goldeneyes, Black Scoters do not concentrate over large mussel beds but appear to utilize shores with gravel and cobbles. They were rarely seen around the rocky shore of Stanley Park, where Surf Scoters and Barrow's Goldeneyes reach high numbers, but were more common on the south shore of English Bay. The coastal habitats used by this species in winter are poorly known, although some inferences can be made based on food habits (Table 5).

The number of Black Scoters recorded in Christmas Bird Counts ranged from 2117 to 3638 between 1975 and 1985, with no apparent trends (Table 7).

5.1.4. Harlequin Duck

Harlequin Ducks are common in the Strait of Georgia in all seasons (Table 10). Numbers drop in May and early June when pairs fly to their breeding sites along inland and coastal rivers. Like most sea ducks, they sometimes concentrate over herring spawns in the spring. Dawe (1976) counted 778 Harlequin Ducks along a rocky shore following a herring spawn. By mid-June, males return to the coast and assemble in groups to moult. Some females moult with their broods inland, but most fly back to the coast where they moult in late summer.

Harlequin Ducks are most concentrated in the summer during the moult period, when they frequent habitat similar to the winter habitat. Moulting groups have been reported from all parts of the Strait of Georgia (Savard 1988*b*). Sites with over 100 moulting birds include Helliwell Park on Hornby Island, Cape Lazo near Comox, Mitlenatch Island, and Oyster and Shelter bays south of Campbell River (Fig. 2). However, large sections of the Strait of Georgia are unsurveyed for Harlequin Ducks.

Because of the large number of birds staying on the coast during the summer, migratory movements are not obvious. The sex ratio of a group of 50 to 90 birds along 3 km of rocky shore near White Rock averaged 1.61 ± 0.10 males per female for the period of November to mid-February ($n = 10$ surveys). Regular counts of this group of birds showed that by mid-May females had left the coast and that the sex ratio for May–August fluctuated between 1.37 and 23.00:1 (Table 10). Mitchell (1952) reported winter sex ratios of 2.13:1, but data from the BC Wildlife Record Scheme yield a ratio of 1.5:1 for the same period. Boat surveys by Vermeer *et al.* (1983) reported Harlequin Ducks in most areas of the Strait of Georgia in March and April but did not record any Harlequin Ducks in the November survey. We suspect this to be an artifact of the survey technique, as Harlequin Ducks should be numerous there in November.

Mitchell (1952) indicated that Harlequin Ducks were seen mostly along unprotected shorelines and that the area of greatest abundance within the Strait of Georgia was the coastline between Qualicum River and Courtenay (Table 1). Numbers observed in Christmas Bird Counts ranged from 774 to 1259 birds between 1975 and 1986, with no obvious trends.

5.2. Seasonal abundance and distribution of four species of shorebirds

The four most common species frequenting rocky shores in winter in the Strait of Georgia are the American Black Oystercatcher (*Haematopus bachmani*), Black Turnstone (*Arenaria melanocephala*), Surfbird (*Aphriza virgata*), and Rock Sandpiper (*Calidris ptilocnemis*).

5.2.1. American Black Oystercatcher

American Black Oystercatchers are abundant in the Strait of Georgia in all seasons and frequent rocky shores almost exclusively (Vermeer, Morgan, and Smith, Part 4, this publication). Little is known of their wintering ecology in the strait. They were seen regularly in only four of the 10 Christmas Bird Counts (Table 11) and were not abundant in any of them. Seasonal movements within the strait have not been well documented. Drent *et al.* (1964) and Vermeer, Morgan, and Smith (Part 4, this publication)

Table 10
Seasonal variation in the sex ratio of Harlequin Ducks near White Rock, British Columbia

Date	No. of males	No. of females	Males/ females
16 November 1980	34	19	1.79
26 November 1980	42	28	1.50
9 December 1980	38	22	1.73
18 December 1980	51	23	2.22
12 January 1981	41	30	1.37
5 February 1981	37	31	1.19
6 May 1981	22	14	1.57
8 May 1981	39	24	1.63
11 May 1981	26	19	1.37
20 May 1981	42	19	2.21
22 May 1981	40	10	4.00
26 May 1981	40	10	4.00
28 May 1981	38	6	6.33
2 June 1981	19	2	9.50
4 June 1981	23	1	23.00
9 June 1981	32	3	10.67
19 June 1981	41	5	8.20
2 July 1981	57	0	
7 July 1981	50	7	7.14
9 July 1981	58	11	5.27
10 July 1981	86	4	21.50
13 July 1981	50	6	8.33
17 July 1981	55	6	9.17
21 July 1981	54	14	3.86
23 July 1981	47	21	2.24
28 July 1981	62	11	5.64
29 July 1981	60	14	4.29
4 August 1981	63	10	6.30
17 August 1981	75	18	4.17
21 August 1981	65	25	2.60
8 October 1986	78	61	1.28
9 October 1986	35	39	0.90
17 October 1986	45	41	1.10
29 October 1986	45	31	1.45
28 November 1986	55	31	1.77
11 December 1986	40	22	1.82
31 December 1986	47	39	1.21
9 January 1986	44	30	1.47
25 April 1986	46	34	1.35
1 May 1986	47	33	1.42
15 May 1986	12	8	1.50
27 May 1986	46	31	1.48
3 June 1986	50	13	3.85
6 July 1986	24	5	4.80
17 July 1986	19	11	1.73
5 August 1986	26	13	2.00

studied aspects of their nesting habitat in the strait. No in-depth studies of the food of oystercatchers have been conducted in either summer or winter (Verbeek and Butler, this publication); however, Butler and Kirbyson (1979) described how nesting birds fed on Pacific oysters (*Crassostrea gigas*) on Mitlenatch Island in the northern part of the strait. Their food on the west coast of Vancouver Island consists chiefly of limpets and mussels, but also of annelids, barnacles, chitons, crabs, isopods, sea cucumbers, and snails (Hartwick 1976; Groves 1982). In the spring, large groups are often found near herring spawning areas (R.W. Campbell, pers. commun.).

5.2.2. *Black Turnstone*

Black Turnstones are the most abundant shorebird wintering on the rocky shores of the Strait of Georgia, where they are observed regularly in highly variable numbers (Tables 6 and 11). Black Turnstones are most abundant within the Strait of Georgia in late April and early May during spring migration (Dawe 1976). According to the BC Wildlife Record Scheme, the postbreeding movement begins in late June and accelerates through the summer. Numbers are highest from September through November and then decrease in December, as some birds move southward. Little is known of their distribution within the strait.

5.2.3. *Surfbird*

Surfbirds winter within the Strait of Georgia, but little is known about their ecology. They frequent inaccessible rocky shores and islands, so that they are seldom observed. Spring staging begins in February and continues through March into April, with the peak movement in late April (R.W. Campbell, pers. commun.). Wintering birds appeared very localized and are seen regularly in only two of the 10 Christmas Bird Counts (Table 11). Nothing is known of the size of the wintering population or its distribution within the strait. Most winter observations are from the Sunshine Coast.

5.2.4. *Rock Sandpiper*

Little is known about the wintering habits of Rock Sandpiper in British Columbia. It is often seen in mixed flocks with Surfbirds and Black Turnstones. Data from the BC Wildlife Record Scheme suggest that it is a late autumn and early spring migrant. It has not been reported regularly in any of the Christmas Bird Counts (Table 6).

5.3. Seasonal abundance and distribution of six species of pelagic birds

Robertson (1977) counted the birds he saw in pelagic waters while traveling on two ferry routes (Tsawwassen to Swartz Bay and Horseshoe Bay to Nanaimo) and offshore of the Gulf Islands during the winter months. He found 3.16 seabirds per square kilometre in the pelagic environment of the Strait of Georgia, which is low compared with the density of seabirds in the pelagic waters off the west coast of Vancouver Island (21.60 seabirds km^{-2}) or shoreline densities of 131.27 seabirds per square kilometre (Robertson 1977). Winter densities were four times those of the summer. Few oceanic species characteristic of the west coast of Vancouver Island were observed in the Strait of Georgia. Gulls, mostly Bonaparte's (*Larus philadelphia*), Mew (*L. canus*), and Glaucous-winged (*L. glaucescens*), comprised the largest proportion of seabirds recorded (Robertson 1977). Incidental surveys suggest that there may be areas with higher densities of seabirds (JPLS, unpubl. data). The tidal currents of Active Pass between Galiano and Mayne islands support high densities of birds throughout the winter (Vermeer 1977). The most abundant species wintering there are the Arctic Loon (*Gavia arctica*) and the Brandt's Cormorant (*Phalacrocorax penicillatus*), whereas the Bonaparte's Gull reaches high numbers there during spring and fall migrations (Vermeer 1977).

Some species of birds frequent deep waters but do not always occur in pelagic waters. I will briefly review here seven species: Western Grebe (*Aechmophorus occidentalis*), Common Murre (*Uria aalge*), Pigeon Guillemot (*Cepphus columba*), Marbled Murrelet (*Brachyramphus marmoratus*), Ancient Murrelet (*Synthliboramphus antiquus*), Rhinoceros Auklets (*Cerorhinca monocerata*), and Oldsquaw.

5.3.1. *Western Grebe*

Western Grebes are present in offshore waters of the Strait of Georgia in all seasons, but mostly in winter (Table 12). They winter in large flocks that feed on school-

Table 11
Average number of shorebirds associated with rocky shores observed in the various Christmas Bird Counts conducted in the Strait of Georgia

	East coast of Vancouver Island						Mainland coast			
Species	**Pender Island**	**Duncan**	**Nanaimo**	**Deep Bay**	**Comox**	**Campbell River**	**Sunshine Coast**	**Vancouver**	**Ladner**	**White Rock**
American Black Oystercatcher	20 ± 7	1 ± 1	14 ± 7	12 ± 4	0	0	15 ± 6	0	0	0
Black Turnstone	37 ± 21	24 ± 10	86 ± 37	204 ± 60	794 ± 467	15 ± 9	63 ± 22	84 ± 21	22 ± 8	14 ± 6
Surfbird	8 ± 7	0	66 ± 25	0	1 ± 1	0	92 ± 30	0	0	0
Rock Sandpiper	0	0	2 ± 1	0	0	0	13 ± 8	0	0	0

Table 12
Average number of some offshore species observed in the various Christmas Bird Counts conducted in the Strait of Georgia

	East coast of Vancouver Island						Mainland coast			
Species	**Pender Island**	**Duncan**	**Nanaimo**	**Deep Bay**	**Comox**	**Campbell River**	**Sunshine Coast**	**Vancouver**	**Ladner**	**White Rock**
Western Grebe	526 ± 297	4045 ± 729	102 ± 42	4926 ± 1632	1655 ± 521	10 ± 6	549 ± 85	5956 ± 546	535 ± 37	44 ± 8
Common Murre	241 ± 64	35 ± 17	37 ± 16	58 ± 19	32 ± 13	2806 ± 966	6 ± 2	15 ± 5	141 ± 29	0
Pigeon Guillemot	12 ± 4	2 ± 1	6 ± 3	5 ± 1	3 ± 2	4 ± 2	1 ± 1	9 ± 1	12 ± 4	1 ± 1
Marbled Murrelet	26 ± 4	40 ± 13	16 ± 4	4 ± 1	6 ± 3	8 ± 5	50 ± 14	135 ± 46	38 ± 12	1 ± 1
Ancient Murrelet	0	0	0	0	0	0	86 ± 79	3 ± 3	0	0

ing fish. The numbers recorded in Christmas Bird Counts vary between areas, ranging from a low of 10 near Campbell River to nearly 6000 near Vancouver. Spring migration occurs mainly from late April to early May, and in March large flocks are seen in areas of actively spawning herring. Small numbers of nonbreeders spend the summer in coastal waters, but little is known of their distribution and ecology. Totals from the Christmas Bird Counts ranged from 9000 to 31 000 birds between 1975 and 1985, with no obvious trends (Table 6).

Western Grebes are very gregarious and occur often in flocks of over 2000 birds; these flocks are well distributed throughout the coastal areas of the strait. In Christmas Bird Counts, large numbers have been reported from Duncan, Deep Bay, and Vancouver. Large flocks are also found in Boundary Bay in winter, and smaller ones during the summer (Savard 1985*b*, and unpubl. data).

5.3.2. *Alcids*

Four species of alcids have been recorded during the Christmas Bird Counts within the Strait of Georgia (Table 12). Their distribution and abundance vary greatly. The Common Murre is the most abundant and most widely dispersed (Vermeer 1977), but large numbers were recorded only near Campbell River in the Christmas Bird Counts. However, large numbers are seen at the mouth of Active Pass outside the breeding season. Pigeon Guillemot and Marbled Murrelet were seen regularly during the Christmas Bird Counts, but in very small numbers. The Ancient Murrelet has been reported only a few times, mostly along the Sunshine Coast (Table 12). Rhinoceros Auklets also winter in the strait but have not been observed in large numbers. The distribution, ecology, and status of these alcids in winter are poorly known.

5.3.3. *Oldsquaw*

Oldsquaw frequent both coastal and pelagic waters of the Strait of Georgia. They are reported in small numbers in almost all Christmas Bird Counts (Table 1). Spring migration begins in late February but is obscured by local movements to herring spawning sites, when flocks of over 3000 birds are seen (e.g., near Qualicum; N.K. Dawe, pers. commun.). Boat surveys in March and April yielded densities ranging between 0.35 and 0.70 birds per kilometre for various areas of the strait (Vermeer *et al.* 1983; Vermeer 1983*b*). Similar surveys in November yielded densities for the same areas of between 0.0 and 0.15 birds per kilometre (Vermeer *et al.* 1983; Vermeer 1983*b*). Some birds spend the summer in the Strait of Georgia (Savard 1988*b*), but no large concentrations have yet been reported.

6. Conclusions

The needs of sea ducks and pelagic birds in the Strait of Georgia are poorly understood. Here, I have sketched the distribution patterns and relative abundance of some species from the little information available. However, their precise requirements in terms of habitat needs remain unknown. Virtually nothing is known about the impact of sea ducks on their own food supply. This has important implications on their management, as some species pose a potential threat to the rapidly expanding aquaculture industry in the Strait of Georgia (Vermeer and Morgan, this publication). Conversely, this industry also threatens these birds, as it could monopolize the best feeding areas.

Little is known about the importance of moulting areas to sea ducks during their vulnerable flightless period. The requirements of moulting sea ducks are unknown, and only a fraction of the Strait of Georgia has been surveyed to locate moulting flocks (Savard 1988*b*). Also, the significance of the interactions between spawning Pacific herring and sea ducks is poorly known. Verbeek (1979) suggested that herring spawn might supply important nutritional needs required by Glaucous-winged Gulls to begin egg laying. Detailed studies on Barrow's Goldeneyes revealed that paired birds used areas different from those used by subadults and unpaired birds. Similar patterns could be found in other species. These preferences in terms of habitats should be documented, as they have important management implications.

Our poor understanding of the abundance, distribution, and ecology of wintering shorebirds in the Strait of Georgia impairs our ability to manage and monitor these species. The abundance and distribution of pelagic birds in the waters of the strait are not well known. Although Common Murres and Marbled and Ancient murrelets have been reported in Christmas Bird Counts, the numbers observed vary greatly from year to year. A greater understanding of their wintering ecology is needed. This may be especially important for the Marbled Murrelet, which could be threatened by logging (Sealy and Carter 1984) and may suffer losses due to gill net fisheries within the strait (Carter and Sealy 1984).

The conservation of shorebirds, sea ducks, and pelagic birds requires a good understanding of their distribution, habitat preferences, and general ecology. For the Strait of Georgia, little is known of the wintering ecology of these birds, especially in terms of habitat use and food preferences. Long-term monitoring of the population levels of these species is also important for proper management. At present, however, it is impossible to develop adequate monitoring methods for most species because of the poor understanding we have of their wintering ecology and their population dynamics.

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The birds of estuaries and beaches in the Strait of Georgia

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1. Abstract

Counts were made of all water birds in eight estuaries and on three beaches in the Strait of Georgia from November to March. The maximum number of birds, using monthly averages, was nearly 118 000 in the estuaries and about 105 000 on the beaches. There was a good relationship between the density of birds and the area of estuaries and beaches that we investigated. Species and bird groups were not evenly distributed. The Fraser River estuary and Boundary Bay beach in the Fraser River delta support most of the waterfowl, wading birds, and gulls, whereas the Cowichan River estuary is a haven for large populations of divers, mostly Western Grebes (*Aechmophorus occidentalis*). However, surveys have not been made of the deeper waters of the Fraser River estuary, so the number of divers might be underrepresented there. There are 43 water bird species that annually occur in estuaries, and 47 species on beaches. In summer, a large portion of the world's population of Western Sandpiper (*Calidris mauri*) uses Boundary Bay, but less is known about other birds at that time of year in most estuaries and beaches.

2. Résumé

Des dénombrements de tous les oiseaux de rivage présents dans huit estuaires et sur trois plages du détroit de Georgia ont été effectués de novembre à mars. D'après les moyennes mensuelles, le nombre maximal d'oiseaux approchait de 118 000 dans les estuaires et il était d'environ 105 000 sur les plages. Une bonne concordance existe entre la densité des oiseaux et l'étendue des estuaires et des plages que nous avons examinés. Les espèces et les groupes d'oiseaux n'étaient pas uniformément distribués. L'estuaire du Fraser et la plage de la baie Boundary dans le delta du Fraser abritaient la majeure partie de la sauvagine, des oiseaux pataugeurs et des goélands et mouettes tandis que l'estuaire de la rivière Cowichan était le refuge de populations importantes d'oiseaux plongeurs, principalement le Grèbe de l'Ouest (*Aechmophorus occidentalis*). Toutefois, des recensements n'ont pas été effectués dans les zones plus profondes de l'estuaire du Fraser, et il est donc possible que le nombre des oiseaux plongeurs soit plus élevé dans cet estuaire. Quarante-trois espèces d'oiseaux aquatiques fréquentent annuellement les estuaires, et 47, les plages. En été, une partie importante de la population mondiale du Bécasseau du Nord-Ouest (*Calidris mauri*) utilise la baie Boundary. On en sait moins sur les autres oiseaux présents à cette époque de l'année dans la plupart des estuaires et sur la plupart des plages du détroit.

3. Introduction

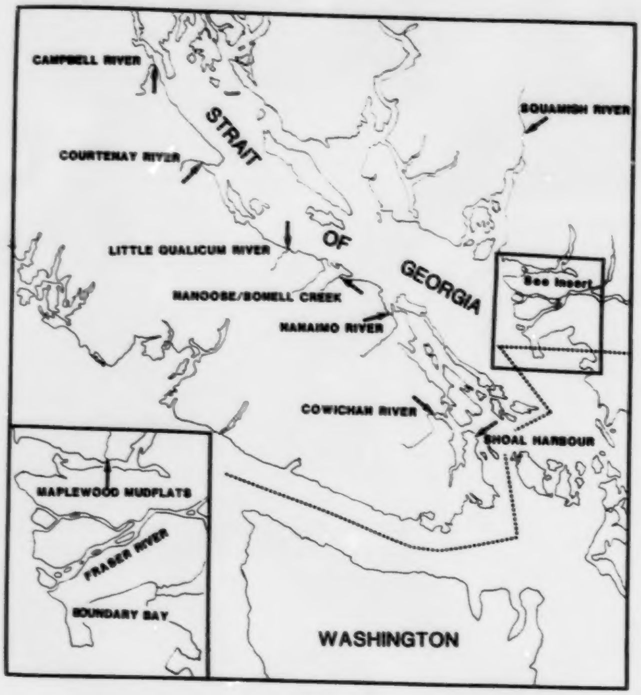
The Strait of Georgia is used by water birds from three continents and more than 20 countries. Along the strait's southeastern shoreline, the largest river in British Columbia—the Fraser River—empties into the Pacific Ocean. A few kilometres south of the Fraser River lies Boundary Bay, which, in concert with the Fraser River estuary, supports internationally significant bird populations (Butler and Campbell 1987). Over 200 creeks and rivers enter the Strait of Georgia, and, although the Fraser River supports the largest bird populations, it does not diminish the importance of other estuaries and beaches.

Bird populations have been counted mostly between November and March in eight estuaries and three beaches in the Strait of Georgia. Most findings appear in government documents (e.g., Environment Canada 1975; Bell and Kallman 1976*a*, 1976*b*; Blood *et al.* 1976; Dawe 1976, 1980, 1982; Morris *et al.* 1979; Dawe and Lang 1980; McKelvey *et al.* 1985; Trethewey 1985; Butler and Campbell 1987). The purpose of this paper is to summarize the findings of those reports and make comparisons among the eight estuaries and three beaches.

4. Study area and methods

The eight estuaries included here are located in the Fraser, Squamish, Campbell, Little Qualicum, Courtenay, Nanaimo, and Cowichan rivers and Nanoose/Bonell Creek (Fig. 1). The three beaches are Boundary Bay, Maplewood Mudflats, and Shoal Harbour (Fig. 1). All estuaries have deltaic marshes, which are described mostly in general terms elsewhere in this volume (Hutchinson *et al.*, this publication). The three beaches are located near estuaries. Boundary Bay lies about 5 km southeast of the Fraser River estuary; Maplewood Mudflats extends about 3 km eastward of the Seymour River mouth in North Vancouver; and small creeks enter Shoal Harbour. We defined the outer limits of all estuaries, except the Fraser River estuary, to be the area within 1 km of the river's mouth or shallower than 3 fathoms (~ 5.5 m), whichever was greater. This arbitrary boundary is about the greatest distance over which birds can be identified from land with a telescope. In the Fraser River estuary, bird surveys included only the marsh and adjacent beach within about 0.5 km of the

Figure 1
Location of estuaries and beaches in the Strait of Georgia where winter bird populations were counted



marsh, because observers were most interested in waterfowl (e.g., Vermeer and Levings 1977; McKelvey *et al.* 1985).

The methods used to estimate bird populations differed among observers and study areas. Birds were counted mostly from aircraft on the Fraser River estuary and in Boundary Bay, whereas birds in other areas were counted from the ground. Most authors summarized their data as monthly means.

The area of each estuary (other than the Fraser River estuary) was traced onto a piece of paper, carefully cut out, and weighed to the nearest 0.001 g on a pan balance. A scale piece cut from the same paper was weighed and used as a proportion to calculate the area of each estuary. The area of the Fraser River estuary included only the brackish marshes within 1 km of the high-tide line and the riverine marshes (Butler and Campbell 1987).

5. The birds—a general picture

5.1. Loons, grebes, and cormorants

The most abundant loons in estuaries are the Common Loon (*Gavia immer*) and Red-throated Loon (*G. stellata*). Neither breeds in the estuaries, but small numbers of *G. stellata* nest on ponds near the coast and feed along its beaches (Pearse 1946). Both species arrive in late September and depart by mid-April. Pacific Loons (*G. pacifica*) are sometimes seen along beaches near eelgrass (*Zostera marina* and *Z. japonica*) beds when Pacific herring (*Clupea harengus*) spawn there in February or March. The four species of grebes that occur in estuaries and on beaches—Horned Grebe (*Podiceps auritus*), Eared Grebe (*P. nigricollis*), Red-necked Grebe (*P. grisegena*), and Western Grebe (*Aechmophorus occidentalis*)—arrive in late September and depart to their breeding areas in April and May. The Double-crested Cormorant (*Phalacrocorax auritus*) is the only abundant estuarine cormorant. It is a resident in the Strait of Georgia (Vermeer, Morgan, and Smith, Part 3, this publication).

5.2. Waterfowl

Two swans—the Trumpeter Swan (*Cygnus buccinator*) and Tundra Swan (*C. columbianus*)—arrive in estuaries from the Alaska breeding grounds in mid-October and depart in March. They precede the peak migration of most dabbling ducks in fall by only a few weeks and similarly depart slightly earlier (McKelvey and Burton 1983). Most Trumpeter Swans spend the winter in BC estuaries (McKelvey 1979), whereas the majority of Tundra Swans spend the winter in the United States. Large winter populations of Mallard (*Anas platyrhynchos*), Northern Pintail (*A. acuta*), Green-winged Teal (*A. crecca*), and American Wigeon (*A. americana*) use both estuaries and beaches, but the Snow Goose (*Chen caerulescens*) seldom departs from estuarine habitats. Most ducks that spend the winter in the coastal estuaries of British Columbia breed in Alaska (R. McKelvey, pers. commun.) and northwestern Canada, whereas the Snow Goose breeds on Wrangel Island in the Soviet Union (Bousfield and Syroechkovskiy 1985). Few species of waterfowl breed in estuaries in the Strait of Georgia—mostly introduced Canada Geese (*Branta canadensis*) and wild Mallard, Blue-winged Teal (*A. discors*), Cinnamon Teal (*A. cyanoptera*), Northern Shoveler (*A. clypeata*), and Gadwall (*A. strepera*) (Butler and Verbeek, this publication). Even fewer diving ducks breed in estuaries, and none nests along its beaches. The most common species of diving duck include the Greater Scaup (*Aythya marila*), Lesser Scaup (*A. affinis*), Surf Scoter (*Melanitta perspicillata*), White-winged Scoter (*M. fusca*), Common Goldeneye (*Bucephala clangula*), Bufflehead (*B. albeola*), Common Merganser (*Mergus merganser*), and Red-breasted Merganser (*M. serrator*). Most diving waterfowl arrive in October and depart in April. Many of these species also frequent rocky coastlines (Savard, this publication).

5.3. Wading birds and shorebirds

Two species of herons occur regularly in estuaries in the Strait of Georgia. The Great Blue Heron (*Ardea herodias*) resides in the strait (Butler, this publication) and feeds in estuaries and along beaches (Verbeek and Butler, this publication). The Green-backed Heron (*Butorides striatus*) recently invaded British Columbia (Campbell 1972). A third ciconiiform, the American Bittern (*Botaurus lentiginosus*), has a more restricted distribution, occurring regularly in small numbers only in the Fraser River estuary (Butler and Campbell 1987). Most shorebirds migrate along beaches and estuaries in the Strait of Georgia. The most abundant migrants include the Black-bellied Plover (*Pluvialis squatarola*), Greater Yellowlegs (*Tringa melanoleuca*), Lesser Yellowlegs (*T. flavipes*), Sanderling (*Calidris alba*), Western Sandpiper (*C. mauri*), Least Sandpiper (*C. minutilla*), Short-billed Dowitcher (*Limnodromus griseus*), and Long-billed Dowitcher (*L. scolopaceus*). The most abundant breeding shorebird is the Killdeer (*Charadrius vociferus*), and the most abundant winter resident is the Dunlin (*Calidris alpina*). Most shorebirds migrate southward from late June to early October and return northward from mid-April to mid-May. Dunlin that winter in the Fraser River delta breed in western Alaska (Greenwood 1984). Similarly, Western Sandpipers banded in western Alaska were captured at the Fraser River delta (G. Kaiser, unpubl. data). Western Sandpipers banded at the Fraser River delta and Sidney Island have been recovered on the central BC coast, in

California, Kansas, Louisiana, Texas, Costa Rica, Mexico, and Suriname. Least Sandpipers banded during the nesting season on the Queen Charlotte Islands by E.H. Miller have been seen on Sidney Island in the Strait of Georgia.

5.4. Gulls and terns

Only one larid, the Glaucous-winged Gull (*Larus glaucescens*), resides in the Strait of Georgia (Vermeer, Part 3, this publication) and uses the estuaries and beaches throughout the year. Large numbers of several other species migrate through the strait, the most abundant being the Bonaparte's Gull (*Larus philadelphia*), Ring-billed Gull (*L. delawarensis*), California Gull (*L. californicus*), and Common Tern (*Sterna hirundo*). Those larids migrate southward from July through October and return in April and May. The Ring-billed Gull is found mostly in the Fraser River estuary and on nearby beaches, but the California Gull uses the entire strait. Both species migrate from their breeding grounds in the Canadian Prairies to the Strait of Georgia in summer (Vermeer 1970; Houston 1977). The Caspian Tern (*S. caspia*) is increasing in abundance along the Pacific coast (Gill and Mewaldt 1983), including the Fraser River delta (Butler and Campbell 1987). The Mew Gull (*Larus canus*) breeds mostly in Alaska, but small numbers nest on lakes on Vancouver Island (Vermeer and Devito 1986), and large numbers winter along its beaches.

6. Bird populations

6.1. Winter

Huge numbers of water birds use the estuaries and beaches in the Strait of Georgia. Totals of the greatest monthly mean reported for each bird group (i.e., divers, waterfowl, wading birds, gulls) show that over 117 000 birds use eight estuaries (Table 1) and about 104 000 use three beaches (Table 2). However, the maximum number tallied in six of those estuaries in which the totals were reported shows that over 400 000 birds can occur in winter (Table 3). Using monthly maximum means (the average of all counts in the month when the species groups were most abundant), we estimated that the winter populations of aquatic birds in the eight estuaries in this study consisted of 5469 divers, 76 521 waterfowl, 22 220 wading birds, and 13 000 gulls, for a total of 117 210 birds (Table 1). Similar estimates for three beaches resulted in 1383 divers, 64 966 waterfowl, 30 670 wading birds, and 7473 gulls, for a total of 104 492 birds (Table 2).

Most of the waterfowl (74.5%) and wading birds (90.0%) counted in estuaries gathered at the Fraser River. A large proportion (30.8%) of gulls also wintered at the Fraser River, but divers were more common on the other estuaries. Nearly half the divers counted were Western Grebes and occurred in largest numbers in the Cowichan River estuary adjacent to the southern Gulf Islands. The extensive marshes and adjacent farmland presumably attract the impressive waterfowl populations in the Fraser River estuary. Similarly, the organic-rich mudflats along the southern end of the Fraser River estuary and adjacent Boundary Bay provide extensive habitat for many birds. The large winter gull population in the Strait of Georgia is composed mostly of the Glaucous-winged Gull, which spends the winter near garbage dumps (Butler *et al.* 1981), and the Mew Gull, which frequents beaches, especially in the Fraser River delta (Butler and Campbell 1987). Divers were the least abundant bird group in all estuaries. However, surveys have not been made of the deeper waters of the Fraser River estuary, where divers would be most abundant.

The Squamish River estuary attracted approximately equal proportions of waterfowl, gulls, and divers (Table 1). Gulls predominated in the Campbell and Nanaimo river estuaries, and waterfowl were the most abundant groups in the relatively large marshes of Courtenay River, Little Qualicum River, Nanoose/Bonell Creek, Cowichan River, and Fraser River estuaries.

Many species were widespread, although in uneven numbers (Table 3). Exceptions include the Pacific Loon, which was found mostly in the Fraser and Little Qualicum river estuaries, and the Red-throated Loon, which occurred in the Fraser, Squamish, and Little Qualicum river estuaries. Double-crested Cormorants were abundant only in the Fraser and Squamish river estuaries, near their breeding colonies (Vermeer and Rankin 1984; Butler and Campbell 1987). Tundra Swans were confined mostly to the Fraser River delta. Wood (1985) found that Common Mergansers concentrated on streams with fish hatcheries, which probably explains the large number of mergansers reported on the Little Qualicum River estuary (Table 3). Most Lesser Snow Geese (*Chen caerulescens caerulescens*), Green-winged Teal, Gadwall, Canvasback (*Aythya valisineria*), Lesser Scaup, Ruddy Ducks (*Oxyura jamaicensis*), and American Coots (*Fulica americana*) were found in the Fraser River estuary.

The number of species using each estuary varied widely (Table 4). The Cowichan and nearby Chemainus river estuaries held 87 species (Bell and Kallman 1976*b*), nearly twice the number (46) in the Seymour River estuary

Table 1
Maximum monthly mean[a] number of water birds counted in estuaries in the Strait of Georgia during winter (1 November – 31 March)

Estuary	Divers[b]	Waterfowl[c]	Wading birds[d]	Gulls	Area (km^2)	Total	Density (birds km^{-2})	References
Fraser	200[e]	57 000	20 000	4 000	12.0	81 200	6766.7	G.W. Kaiser, unpubl. data; McKelvey *et al.* 1985
Squamish	522	740	30	568	3.2	1 860	581.3	Trethewey 1985
Campbell	180	496	35	1 118	2.0	1 829	914.5	Trethewey, unpubl. data
Courtenay	370	5 517	1 008	1 597	6.7	8 492	1267.5	Trethewey 1979
Little Qualicum	204	2 483	87	812	1.1	3 586	3260.0	Dawe 1976, 1980, unpubl. data
Nanoose/Bonell	546	1 110	30	552	1.0	2 238	2238.0	Dawe and Lang 1980
Nanaimo	900	1 050	34	2 400	17.0	4 384	257.9	Bell and Kallman 1976*a*
Cowichan[f]	2547	8 125	996	2 545	8.0	14 213	1776.6	Blood *et al.* 1976
Total	**5469**	**76 521**	**22 220**	**13 000**		**117 210**		

[a] Maximum monthly mean = the greatest monthly mean reported per species summed for all species of divers, waterfowl, wading birds, and gulls.

[b] Loons, grebes, cormorants, and alcids.

[c] Swans, geese, ducks, and coots.

[d] Herons and shorebirds.

[e] McKelvey *et al.* (1985) did not survey deep water where most divers occur.

[f] McKelvey *et al.* (1985) surveyed a strip of estuary about 800 m wide and 15 km long (R.W. McKelvey, pers. commun.).

Table 2
Maximum monthly mean[a] number of water birds counted on beaches in the Strait of Georgia during winter (31 October – 31 March)

Beach	Diver[b]	Waterfowl[b]	Wading birds[b]	Gulls	Area (km^2)	Total	Density (birds km^{-2})	References
Boundary Bay	1000	60 000	29 600	6200	63.6	96 800	1522.0	Savard 1985; McKelvey *et al.* 1985
Maplewood Mudflats	140	3 500	1 000	1100	0.9	5 740	6377.8	Environment Canada 1975
Shoal Harbour[c]	243	1 466	70	173	1.2	1 952	1626.7	Dawe 1982
Total	**1383**	**64 966**	**30 670**	**7473**		**104 492**		

[a] Maximum monthly mean = the greatest monthly mean reported per species summed for all species of divers, waterfowl, wading birds, and gulls.
[b] Same bird groups as in Table 1.
[c] Mean for October–April.

Table 3
Maximum number of individuals of abundant (≥ 100) bird species ever counted during winter (1 November – 31 March) in estuaries in the Strait of Georgia

Species	Fraser[a]	Squamish[b]	Campbell[c]	Qualicum[d]	Nanoose/[e] Bonell	Nanaimo[f]
Red-throated Loon	140	12	0	10	0	0
Pacific Loon	197	0	0	55	1	0
Common Loon	119	15	2	34	7	30
Horned Grebe	293	109	61	14	13	59
Red-necked Grebe	227	23	1	8	6	21
Western Grebe	1 067	772	50	510	700	900
Double-crested Cormorant	336	70	0	3	1	1
Great Blue Heron	251	13	11	4	7	48
Tundra Swan	125	0	0	1	0	15
Trumpeter Swan	150	5	2	70	9	1
Snow Goose	40 000	0	0	100	1	0
Brant	0	0	0	2 600	0	0
Canada Goose	1 000	7	0	30	1	9
Green-winged Teal	50 000	79	2	150	14	23
Mallard	50 000	188	85	811	100	182
Northern Pintail	35 000	113	0	4	32	343
Gadwall	132	0	0	2	2	0
American Wigeon	62 000	93	4	544	680	463
Canvasback	753	2	0	0	0	1
Greater Scaup	3 003	38	4	189	161	45
Lesser Scaup	248	0	0	0	0	0
Black Scoter	493	0	3	307	20	12
Surf Scoter	1 684	9	1	385	94	187
White-winged Scoter	477	0	350	182	242	210
Common Goldeneye	450	229	61	300	69	122
Barrow's Goldeneye	87	58	0	0	11	42
Bufflehead	1 143	113	179	150	24	183
Common Merganser	177	129	16	300	7	153
Red-breasted Merganser	249	56	8	16	42	74
Ruddy Duck	3 838	0	0	2	0	0
American Coot	760	0	2	1	10	2
Black-bellied Plover	727	0	0	0	0	0
Killdeer	411	6	3	23	15	7
Dunlin	109 000	0[g]	0	132	0	190[g]
Bonaparte's Gull	1 053	0	0	3 000	0	0
Mew Gull	7 243	0	40	250	255	0
Thayer's Gull	924	0	62	960	720	0
Glaucous-winged Gull	30 000	1118[h]	1142[i]	1 500	230	4160[j]
Marbled Murrelet	107	14	0	0	10	3
Northwestern Crow	ND[k]	296	222	130	360	424
Total	**403 864**	**3564**	**2311**	**12 640**	**3835**	**7910**

[a] Maximum from Ladner Christmas Bird Count or aerial survey reported in Butler and Campbell (1987).
[b] Data from Appendix 2.2 in Trethewey (1985).
[c] Data from Trethewey (unpubl.).
[d] Data from Dawe (1976, 1980, unpubl.) and Eamer 1985.
[e] Data from Dawe and Lang (1980) and Eamer 1985.
[f] Data from Environment Canada (1973).
[g] Unidentified shorebirds were probably Dunlin.
[h] Trethewey (1985) reported 1118 gulls that were probably Glaucous-winged Gulls.
[i] Trethewey (unpubl. data) reported 1142 gulls at Campbell River estuary that were probably Glaucous-winged Gulls.
[j] Maximum gulls reported in February were probably mostly Glaucous-winged Gulls.
[k] ND = no data, but probably occur in numbers < 100.

(Environment Canada 1975). Waterfowl were most diverse, followed by waders, divers, and gulls. The relative diversity (J' in Table 4) of those bird groups ranged from 0.888 at the Seymour River estuary to 0.946 at the Cowichan River estuary. An estuary with every species would have a value of 1.0.

Published accounts of birds on beaches are not as thorough as those dealing with estuaries. Dawe (1982) listed 41 species of marine birds that he saw at Shoal Harbour, and Environment Canada (1975) listed 46 species for Maplewood Mudflats. About 47 species regularly use beaches, and 43 species use estuaries in winter. Three species unique to beaches at Shoal Harbour (Harlequin Duck [*Histrionicus histrionicus*], Black Turnstone [*Arenaria melanocephala*]) and Maplewood Mudflats (Marbled Murrelet [*Brachyramphus marmoratus*]) occur most commonly on rocky

Table 4
The number of species of divers, waterfowl, wading birds, and gulls[a] and diversity[b] reported in eight estuaries in the Strait of Georgia

	Squamish		Cowichan		Nanaimo		Campbell		Courtenay		Fraser		Seymour		Little Qualicum	
Bird group	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Divers	14	18.2	15	17.2	15	17.7	12	21.8	14	18.7	14	17.7	10	21.7	15	18.5
Waterfowl	34	44.2	34	39.1	34	40.0	25	45.5	33	44.0	33	41.8	23	50.0	31	38.3
Wading birds	19	24.7	26	29.9	25	29.4	11	20.0	19	25.3	22	27.8	6	13.1	23	28.4
Gulls	10	12.9	12	13.8	11	12.9	7	12.7	9	12.0	10	12.7	7	15.2	12	14.8
Total	**77**	**100.0**	**87**	**100.0**	**85**	**100.0**	**55**	**100.0**	**75**	**100.0**	**79**	**100.0**	**46**	**100.0**	**81**	**100.0**
H'	0.557		0.567		0.563		0.554		0.555		0.560		0.534		0.534	
J'	0.925		0.946		0.935		0.920		0.921		0.930		0.888		0.923	

[a] Bird groups are defined in Table 1.
[b] Diversity values are as follows:
H' is the Shannon-Weaver Index (Zar 1984).
J' is the relative diversity = H'/H'_{max}, where H'_{max} is the maximum possible diversity. Here H'_{max} = 0.602.

shores that surround the beaches (Savard, this publication), but one species—the Ruddy Duck—appears to select mudflat habitats. It was abundant in Boundary Bay and present in smaller numbers at Shoal Harbour and Maplewood Mudflats. Six species appear to choose estuaries over beaches, although using both: the Tundra Swan, Trumpeter Swan, Lesser Snow Goose, Canvasback, Lesser Scaup, and Common Merganser.

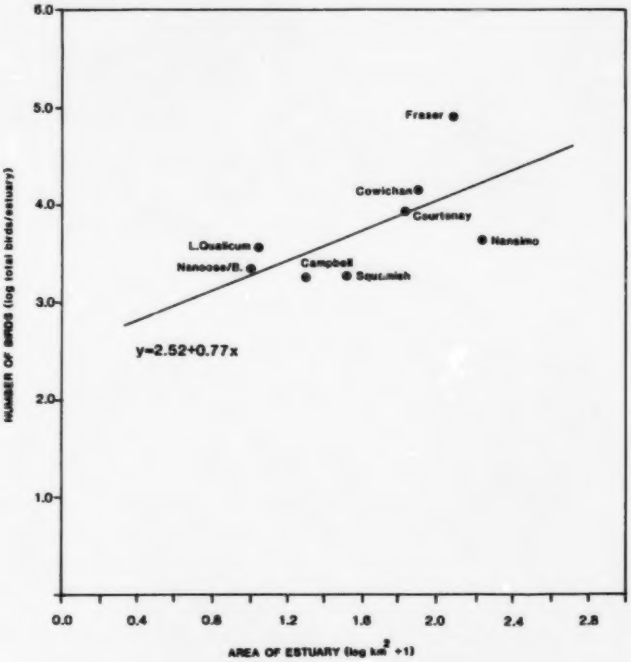
The number of birds using an estuary increased with the size of the estuary (Fig. 2), although the density of birds was generally greater on the smaller estuaries (Table 1). For example, the Courtenay River estuary supported nearly four times as many birds as the Nanoose/Bonell Creek estuary, but in an area almost seven times as large. An exception to this pattern was the Fraser River estuary, which had very high densities of birds.

6.2. Summer

Less is known about bird populations in estuaries and on beaches along the Strait of Georgia in summer than in winter. Butler and Campbell (1987) showed that the average monthly mean estimates of waterfowl in the Fraser River estuary in summer were less than 10% of the annual numbers. At the Little Qualicum River estuary, Dawe (unpubl. data) found that the maximum number of waterfowl in summer was 6% of the winter population. Of 104 water bird species reported to occur annually on the Fraser River estuary, 33 (31.7%) bred there, mostly in small numbers (Butler and Campbell 1987). The nesting population of water birds on the Fraser River estuary is dominated by the Double-crested Cormorant, Great Blue Heron, Canada Goose, Mallard, Blue-winged Teal, Cinnamon Teal, Gadwall, Killdeer, and Glaucous-winged Gull. During the southward migration of shorebirds between July and September 1975, Blood *et al.* (1976) counted 1273 shorebirds of 13 species in the Cowichan Bay area. Western Sandpipers were most common (34.6%), followed by Killdeer (24.5%), Long-billed Dowitcher (10.3%), Spotted Sandpiper (*Actitis macularia*, 5.5%), and Pectoral Sandpiper (*Calidris melanotos*, 6.1%).

Information on bird populations on most beaches in the Strait of Georgia during summer is also scant. At a 96-ha lagoon on Sidney Island in the southern end of the Strait of Georgia, Butler (unpubl. data) recorded 41 species in the summers of 1985–87. The only published study of a beach species in the strait during summer dealt with the migration of the Western Sandpiper at Sidney Island and Boundary Bay (Butler *et al.* 1987). Adult sandpipers migrated north in April and May and south from late June to late July. Juveniles followed between late July and early October. Adult males preceded females in spring but migrated after them in autumn. The length of stay of individual Western Sandpipers at Sidney Island was 2–3 d on average.

Figure 2
Relationship between the number of birds counted in winter and area of eight estuaries in the Strait of Georgia



7. The significance of estuaries and beaches

Some species rely heavily on estuaries and beaches for their survival at certain times of the year. When upland feeding sites freeze in winter, grazing waterfowl take refuge in Vancouver Island estuaries (Dawe 1980; Eamer 1985).

The Convention on Wetlands of International Importance, especially as Waterfowl Habitat (known as the Ramsar Convention), uses selection criteria that include sites that support:

(1) 10 000 ducks, geese, and swans; or 10 000 coots; or 20 000 waders; or

(2) 1% of the individuals of one species or subspecies of waterfowl; or
(3) 1% of the breeding pairs in a population of one species or subspecies of waterfowl.

Under those criteria, the Fraser River estuary and the beaches in Boundary Bay qualify many times over as wetlands of international importance (Butler and Campbell 1987). The remaining estuaries and beaches in which counts have been made do not qualify as sites of international significance under the Ramsar criteria. National criteria have not been established, and, until estimates are made in other BC estuaries, it is impossible to rank them. However, because few places in Canada support as many birds in winter as the BC estuaries and beaches, those sites as a group are probably significant in the conservation of birds in western Canada.

8. Conclusions

The Strait of Georgia supports the largest population of water birds in Canada during winter. Estuaries have long been considered vital to the survival of those large bird populations. Our findings strongly suggest that some beaches near estuaries may be equally important. The largest estuary and beach habitat occurs in the Fraser River delta. We urge that measures be quickly taken to secure those habitats for the preservation of internationally significant bird populations. We also emphasize that several estuaries are needed to protect the variety of water birds in the strait. In addition, some beaches must be recognized for their importance to the survival of many shorebirds.

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Marine birds of Jervis Inlet, a mainland fjord entering the Strait of Georgia

Kees Vermeer

1. Abstract

Marine bird populations were surveyed from August 1986 through June 1987 in Jervis Inlet. The population was small in summer (1–5 birds km^{-2}), increased in September (8 birds km^{-2}), was highest from October through March (25–44 birds km^{-2}), and decreased again in April and May (13–16 birds km^{-2}). The two most numerous species present were Barrow's Goldeneyes (*Bucephala islandica*) and Surf Scoters (*Melanitta perspicillata*). Several epibenthic or benthic-feeding species, such as Pigeon Guillemots (*Cepphus columba*) and White-winged Scoters (*Melanitta fusca*), were scarce in Jervis Inlet, which is too deep for benthic feeding. Known foragers on herring in the Strait of Georgia, such as Pacific Loons (*Gavia immer*), Western Grebes (*Aechmophorus occidentalis*), Brandt's Cormorants (*Phalacrocorax penicillatus*), and Common Murres (*Uria aalge*), were also relatively scarce (or absent) in Jervis Inlet.

Birds occurred in five habitats: the open-water zone (104.3 km^2), rocky shores (62.6 km^2), estuaries (7.2 km^2), log storage sites (2.4 km^2), and Malibu Rapids (0.6 km^2). Average bird densities in these habitats were 2.4, 62.6, 96.3, 83.2, and 228.0 birds per square kilometre, respectively. Barrow's Goldeneyes and Surf Scoters were the most numerous birds along rocky fjord walls. Dabbling ducks, Common Goldeneyes (*Bucephala clangula*), Mew Gulls (*Larus canus*), and Western Grebes had highest densities in estuaries, and Horned (*Podiceps auritus*) and Red-necked (*P. grisegena*) grebes and Bonaparte's Gulls (*Larus philadelphia*) had highest densities at log storage sites.

2. Résumé

Les populations d'oiseaux marins de l'inlet Jervis ont été étudiées d'août 1986 à juin 1987. La densité était faible en été (1–5 oiseaux au km^2), augmentait en septembre (8 oiseaux au km^2), était maximale d'octobre à mars (25–44 oiseaux au km^2) et diminuait de nouveau en avril et mai (13–16 oiseaux au km^2). Les deux espèces les plus abondantes étaient le Garrot de Barrow (*Bucephala islandica*) et la Macreuse à front blanc (*Melanitta perspicillata*). Plusieurs espèces se nourrissant d'organismes épibenthiques ou benthiques, comme le Guillemot du Pacifique (*Cepphus columba*) et la Macreuse à ailes blanches (*Melanitta fusca*), ont été rarement observées dans l'inlet qui est trop profond pour ces espèces qui s'alimentent sur le fond. D'autres espèces qui sont des consommateurs connus du hareng du détroit de Georgia, comme le Huard à collier (*Gavia immer*), le Grèbe de l'Ouest (*Aechmophorus occidentalis*), le Cormoran de Brandt (*Phalacrocorax penicillatus*) et la Marmette commune (*Uria aalge*), étaient également relativement rares (ou absentes).

Les oiseaux ont été observés dans cinq types d'habitat : la zone d'eau libre (104,3 km^2), les rivages rocheux (62,6 km^2), les estuaires (7,2 km^2), les zones d'entreposage de bois (2,4 km^2) et les rapides Malibu (0,6 km^2). Les densités moyennes dans ces habitats s'élevaient respectivement à 2,4, 62,6, 96,3, 83,2 et 228,0 oiseaux au kilomètre carré. Les Garrots de Barrow et les Macreuses à front blanc étaient les espèces les plus abondantes sur les parois rocheuses des fjords. Les oiseaux observés plus fréquemment étaient, dans les estuaires, les canards de surface, le Garrot commun (*Bucephala clangula*), le Goéland cendré (*Larus canus*) ainsi que le Grèbe de l'Ouest et, aux lieux d'entreposage de bois, le Grèbe cornu (*Podiceps auritus*), le Grèbe jougris (*P. grisegena*) et la Mouette de Bonaparte (*Larus philadelphia*).

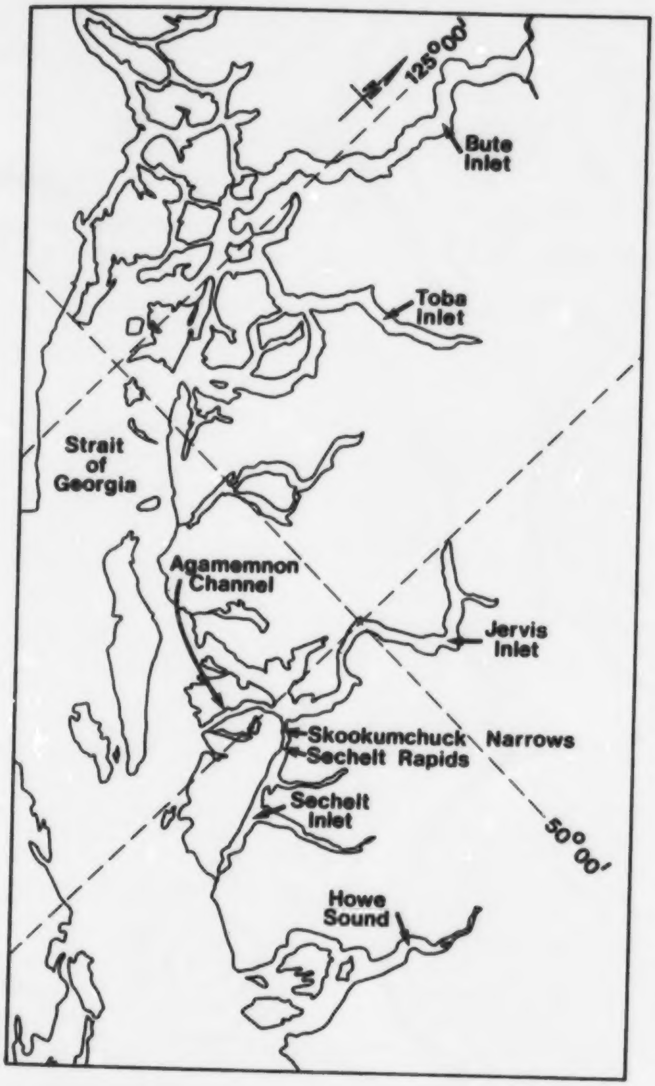
3. Introduction

Previous observations suggested that Barrow's Goldeneyes (*Bucephala islandica*) and Surf Scoters (*Melanitta perspicillata*) were the most numerous water birds in the mainland fjords of British Columbia (Vermeer 1981; Vermeer *et al.* 1983). Little is known, however, of the overall and seasonal marine bird composition in those fjords. To determine the composition and seasonal changes of the bird population present, I surveyed Jervis Inlet from August 1986 to June 1987.

4. Description of study area

Jervis Inlet is one of four mainland fjords entering the Strait of Georgia from the east (Fig. 1). Jervis Inlet enters the strait by two channels—one large unnamed channel and Agamemnon Channel. These two channels are joined by Sechelt Inlet, a tributary fjord, which enters Jervis Inlet through Skookumchuk Narrows, before the inlet takes on the typical form of a long and narrow BC fjord, unadorned by large embankments and islands (Fig. 1). It was this long and narrow portion of Jervis Inlet, from a line connecting Foley Head and Egmont Point to the Skwawka River estuary at the head (Fig. 2), that was surveyed. This body of water consists of three sections: Prince of Wales Reach, Princess Royal Reach,

Figure 1
Location of Jervis Inlet in relation to other BC fjords entering the Strait of Georgia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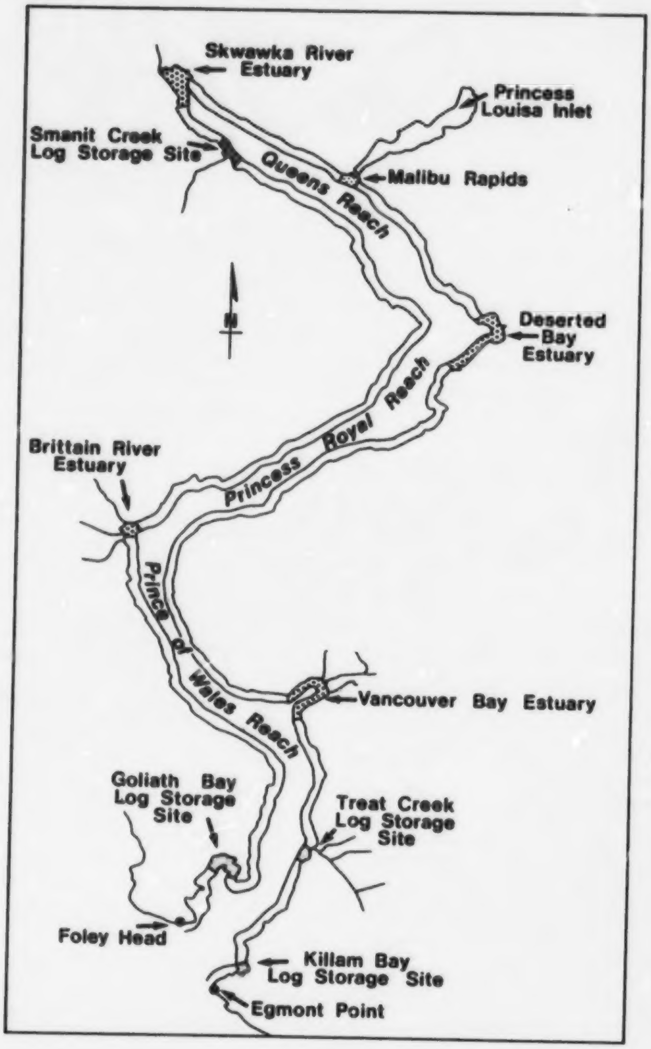
Toba Inlet
Strait of Georgia
Agamemnon Channel
Jervis Inlet
Skookumchuck Narrows
Sechelt Rapids
Sechelt Inlet
50°00'
Howe Sound

Figure 2
The section of Jervis Inlet in which marine birds were surveyed from August 1986 through June 1987


Skwawka River Estuary
Princess Louisa Inlet
Smanit Creek Log Storage Site
Queens Reach
Malibu Rapids
N
Deserted Bay Estuary
Princess Royal Reach
Brittain River Estuary
Prince of Wales Reach
Vancouver Bay Estuary
Goliath Bay Log Storage Site
Treat Creek Log Storage Site
Foley Head
Killam Bay Log Storage Site
Egmont Point

and Queens Reach. Princess Louisa Inlet, a small inlet entering Queens Reach, was not surveyed.

The physical oceanography of BC mainland fjords has been described by Pickard (1961), and that of Jervis Inlet is briefly summarized here. The most significant influence in the fjord is the freshwater runoff, chiefly from rivers, creeks, and waterfalls. The runoff is nonglacial, and the water is generally clear. Depending on the amount of rainfall, the runoff occurs mostly from late autumn to spring. The surface salinity increases from zero at the head of the inlet to coastal sea values at the mouth. In winter the surface temperature is low and uniform, but in summer it increases from the head. The water is highly stratified, particularly from the surface to about 20 m depth, where the salinity rises to 90%. Below 50 m, the salinity and temperature do not change much. The mean mid-inlet depth of Jervis is 495 m, with a maximum depth of 666 m, which is deeper than any part of the Strait of Georgia.

The surveyed section of Jervis Inlet is bound by precipitous rock walls through which creeks and streams have carved gullies. The intertidal area consists mostly of a cliff face, and beaches are generally nonexistent, except where there are estuaries. Small estuaries, with gravel and mud beaches, are found where small rivers enter the inlet—at Deserted and Vancouver bays, at the head of Jervis Inlet, and at Brittain River (Fig. 2). The shores are predominantly forested. Most of the original forest has been logged, but patches of old growth remain. The only localities inhabited by people occur at Egmont Point, the four estuaries, Malibu Rapids, and four logging camps with log storage sites (at Goliath Bay, Smanit Creek, Killam Bay, and the Treat Creek area; Fig. 2) covering the adjacent waterfronts.

5. Methods

Jervis Inlet was surveyed by boat once each month from August 1986 through June 1987, except in February. Surveys were conducted by two observers within 0.5 km of the shoreline, along the whole length of the inlet. The surveys began at Foley Head and continued from there to the Skwawka River estuary at the head of Jervis Inlet;

the return route was from there along the other shore to Egmont Point (Fig. 2). Each survey, lasting about 9 h, was conducted at a speed ranging from 20 to 30 km·h^{-1}, with stops to count birds where they were congregated.

Jervis Inlet was divided into the open-water zone, which was the water surface area beyond 0.5 km from the shoreline, and the following zones all within 0.5 km of shoreline: rocky shore zone, estuaries, log storage sites, and Malibu Rapids (Fig. 2). All birds were counted in the five habitat zones separately. The total water surface area of Jervis, as well as that of each of the five habitats, was measured with a planimeter on a 1:50 000 scale hydrographic chart of Jervis Inlet (No. 3514). The numbers of birds counted were divided by the measured water surface areas to obtain bird densities. In a few cases where sample size was adequate, Kruskal-Wallis and nonparametric multiple range tests were applied to determine if bird densities between habitats were significantly different.

6. Results

6.1. Bird composition and seasonal changes

The largest number and species of birds, as well as the highest densities, were seen from October through March; numbers and bird densities declined in April and May; in June and August they dwindled to a small fraction of what they were in the winter (Table 1). Of four major groups of birds, waterfowl were most numerous from October through May, and gulls in June, August, and September (Fig. 3). The two smallest bird categories present in Jervis Inlet were those of loons, grebes, and cormorants, and auks.

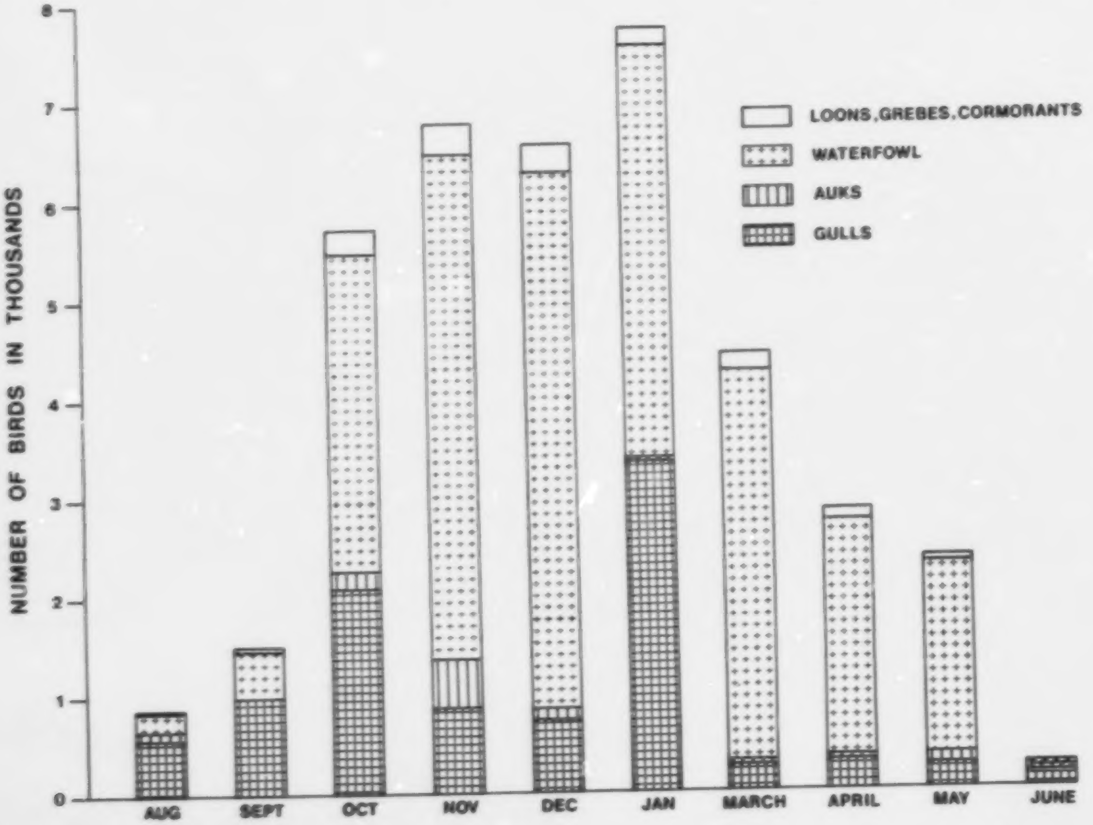
Of the loons, the Common Loon (*Gavia immer*) was the main species seen (Fig. 4). Pacific Loons (*G. pacifica*) were encountered only twice, two in October and one in December. Of the grebes, the Horned Grebe (*Podiceps auritus*) and Red-necked Grebe (*P. grisegena*) were most common, except in May, when more Western Grebes (*Aechmophorus occidentalis*) were observed. Pelagic (*Phalacrocorax pelagicus*) and Double-crested (*P. auritus*) cormorants were common from October through May.

The waterfowl category was divided into three groups: swans, geese, and dabbling ducks; mergansers; and

Table 1
Number of species, number of birds, and bird densities observed in Jervis Inlet, August 1986 – June 1987

Month	No. of bird species	No. of birds	Birds km^{-2}
August	11	863	4.88
September	15	1 498	8.46
October	24	5 718	32.30
November	23	6 763	38.20
December	24	6 586	37.20
January	20	7 727	43.64
March	19	4 442	25.09
April	18	2 825	15.96
May	18	2 391	13.45
June	8	254	1.43
Total no. of birds		**39 067**	
Average density			**22.06**

Figure 3
Seasonal changes in the composition of major bird groups in Jervis Inlet



diving ducks (Fig. 5). In the first group, the Mallard (*Anas platyrhynchos*) was most common, followed by the American Wigeon (*A. americana*). Of the mergansers, the Common Merganser (*Mergus mergus*) was most numerous and was one of the few bird species that occurred less in winter than in any other season. Of all birds, two species of diving ducks—the Surf Scoter and Barrow's Goldeneye—were most numerous, the former from October through January and the latter from November through April. Other common diving ducks were Bufflehead (*Bucephala albeola*) and Common Goldeneye (*B. clangula*), whereas only a few Harlequin Ducks (*Histrionicus histrionicus*) and Greater Scaup (*Aythya marila*) were seen, and only once a Black Scoter (*Melanitta nigra*) and a White-winged Scoter (*M. fusca*).

The Marbled Murrelet (*Brachyramphus marmoratus*) was the main auk present (Fig. 6). Murrelets were most common in October and November, and another peak occurred in May. Marbled Murrelets were one of the few species that were common in summer. Young murrelets accompanied by parents were observed twice in August. In January, only 46 murrelets were seen in Jervis Inlet, but 180 were counted just outside the inlet, between Egmont Point and Egmont. A flock of 1800 murrelets was seen on 1 April 1977 in the same area near Egmont Point (KV, pers. obs.). Pigeon Guillemots (*Cepphus columba*) and Common Murres (*Uria aalge*) were seen only twice (one and two individuals).

Of the gulls, the Glaucous-winged Gull (*Larus glaucescens*) was one of the two most common species. They were most numerous in September and October (Fig. 6). On average, 68% were adults and 32% immatures (Table 2). Of the immatures seen in September, 84% were young-of-the-year. Because no Glaucous-winged Gulls were observed to nest in Jervis Inlet, adults and young likely dispersed from their colonies in the Strait of Georgia, where they nest in large numbers (Vermeer and Devito, this publication), into Jervis Inlet.

The other numerous gull species was the Mew Gull (*Larus canus*) (Fig. 6). In January, one large flock of 2500 Mew Gulls was seen together with a flock of about 165 Bonaparte's Gulls (*L. philadelphia*). California Gulls (*L. californicus*) were seen in Jervis Inlet only in late summer and early autumn. A few Herring Gulls (*L. argentatus*) and Ring-billed Gulls (*L. delawarensis*) were also observed.

6.2. Bird densities related to habitat

The largest habitats in Jervis Inlet are the open-water and rocky shore zones, whereas estuaries, log storage sites, and the Malibu Rapids make up only a small fraction of the total water habitat (Table 3). Although the largest number of birds was observed along rocky shorelines (Fig. 7), higher bird densities were found at log storage sites, estuaries, and the Malibu Rapids (Fig. 7). Overall bird densities were significantly smaller in open water than at estuaries, log storage sites, rocky shores, and Malibu Rapids, whereas those at rocky shores were also significantly smaller than those at the rapids (Table 4).

Bird densities varied according to species in each of the five habitats (Table 5). All species had their lowest densities in open water. Of all birds, Barrow's Goldeneyes and Surf Scoters had by far the highest densities along rocky shores (Table 5). The distribution of numbers and densities of those two species showed a similar trend for the different habitats, except for log storage sites, where significantly more Barrow's Goldeneyes occurred than Surf Scoters (Fig. 8). Barrow's Goldeneyes had significantly lower densities in open water than at log storage sites and Malibu Rapids, and Surf Scoters had significantly lower densities in open water than at rocky shores and the rapids (Table 4).

Most Glaucous-winged Gulls also occurred along rocky shores (Fig. 8), but their densities were significantly higher at log storage sites, estuaries, and the Malibu Rapids (Table 4). Of all birds, Glaucous-winged Gulls had the highest densities at the rapids (Table 5). Other species with high densities at the rapids were Pelagic and Double-crested cormorants, Bufflehead, and California Gulls. Red-necked and Horned grebes and Bonaparte's Gulls had their highest densities at log storage sites; Western Grebes, Mallards, American Wigeon, Common Goldeneyes, Common Mergansers, and Mew Gulls had their highest densities in estuaries; and Marbled Murrelets had similar densities in both estuaries and log storage sites (Table 5).

6.3. Bird movement in Jervis

6.3.1. Barrow's Goldeneyes and Surf Scoters

A record was kept of locations where flocks of Barrow's Goldeneyes and Surf Scoters were seen feeding or resting in Jervis Inlet during each survey. Those two species frequently occurred in mixed flocks. From August

Figure 4
Seasonal changes in numbers of loons, grebes, and cormorants in Jervis Inlet

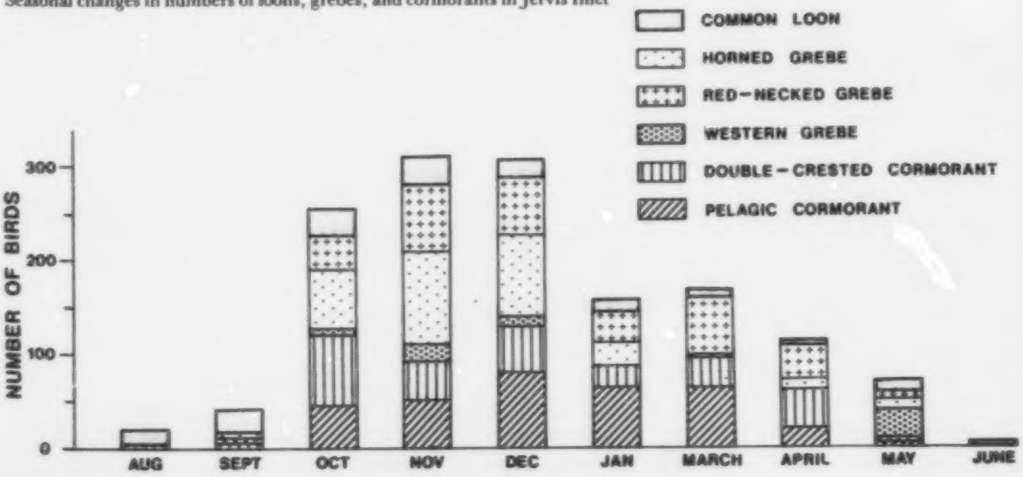
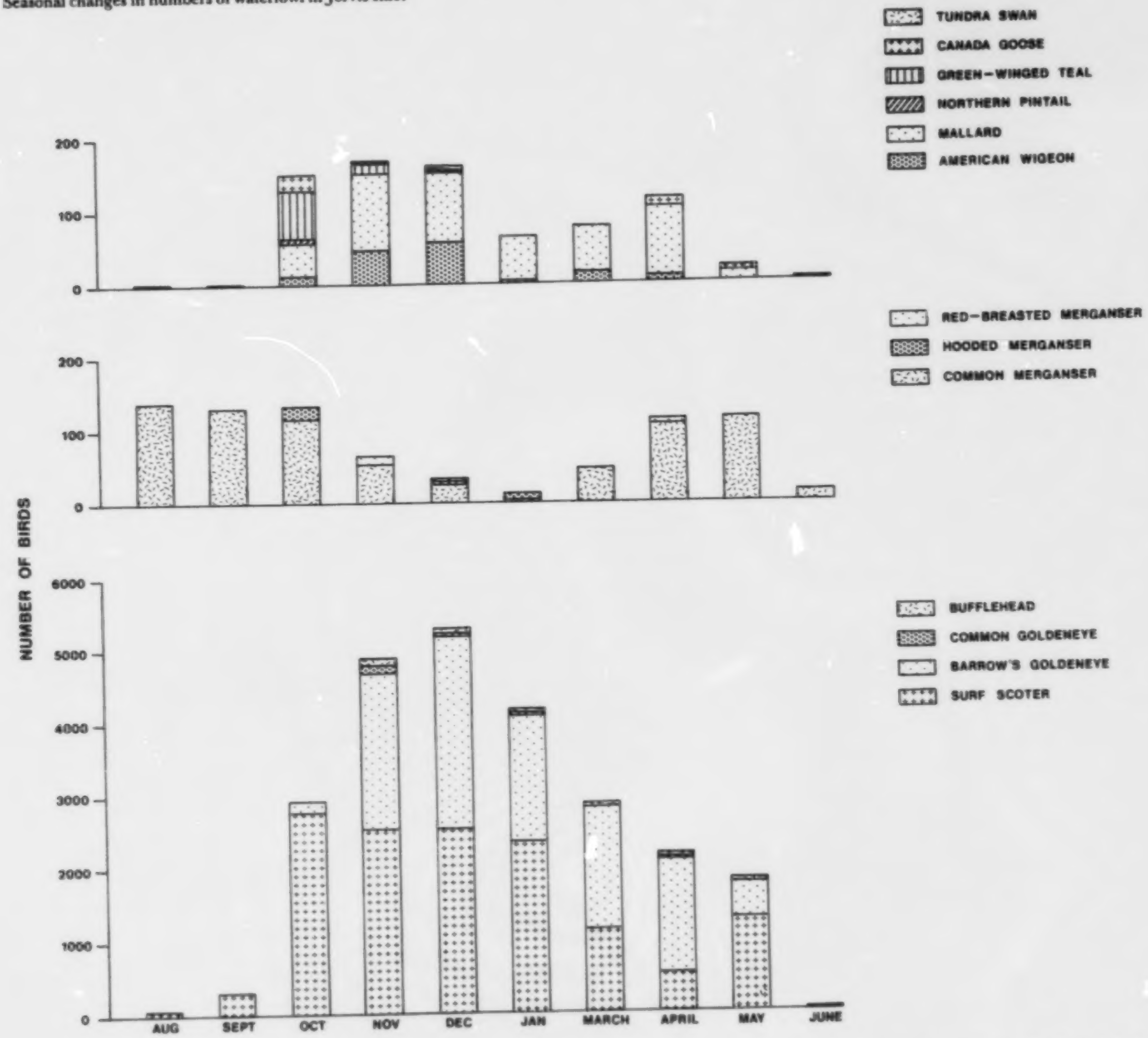


Figure 5
Seasonal changes in numbers of waterfowl in Jervis Inlet



through October, both species occurred mostly in Queens Reach; by November, large numbers of those ducks had moved into Princess Royal Reach; and from December through March, they were also common in the upper portion of Prince of Wales Reach (Table 6). On average, higher bird densities occurred in Queens and Princess Royal reaches than in Prince of Wales Reach (Table 6).

6.3.2. Common Mergansers

Common Mergansers seen from August until January were either females or immatures. In autumn, the mergansers concentrated mostly at the mouth of streams entering Jervis Inlet. In spring, the composition of mergansers had drastically changed; about an equal number of males and females were observed in pairs, and they were dispersed along the whole of Jervis Inlet.

6.3.3. Bonaparte's and Mew gulls

Bonaparte's and Mew gulls were mostly seen in estuaries and log storage sites (Table 5). In January, however, a flock of 2500 Mew Gulls was seen in the vicinity of Vancouver Bay. Of those 2500 gulls, about 1000 were in the Vancouver Bay estuary, and another 1500 were observed feeding and resting in the open-water zone outside Vancouver Bay. A smaller flock of 165 Bonaparte's Gulls accompanied the Mew Gulls in the open-water zone. The flock of Mew Gulls was the largest one of all birds observed in open water. In April, only 132 Mew and no Bonaparte's gulls were seen in Jervis Inlet, but 1100 Bonaparte's and 250 Mew gulls were seen feeding on euphausiids at Sechelt Rapids, which is close to Jervis Inlet (Fig. 2).

7. Discussion

7.1. The importance of the rocky shore zone to goldeneyes and scoters

The surveys indicate that Jervis Inlet is chiefly utilized by birds from autumn to spring, whereas few birds occur in summer. They also support preliminary findings that the two most numerous bird species in Jervis Inlet

Figure 6
Seasonal changes in numbers of auks and gulls in Jervis Inlet

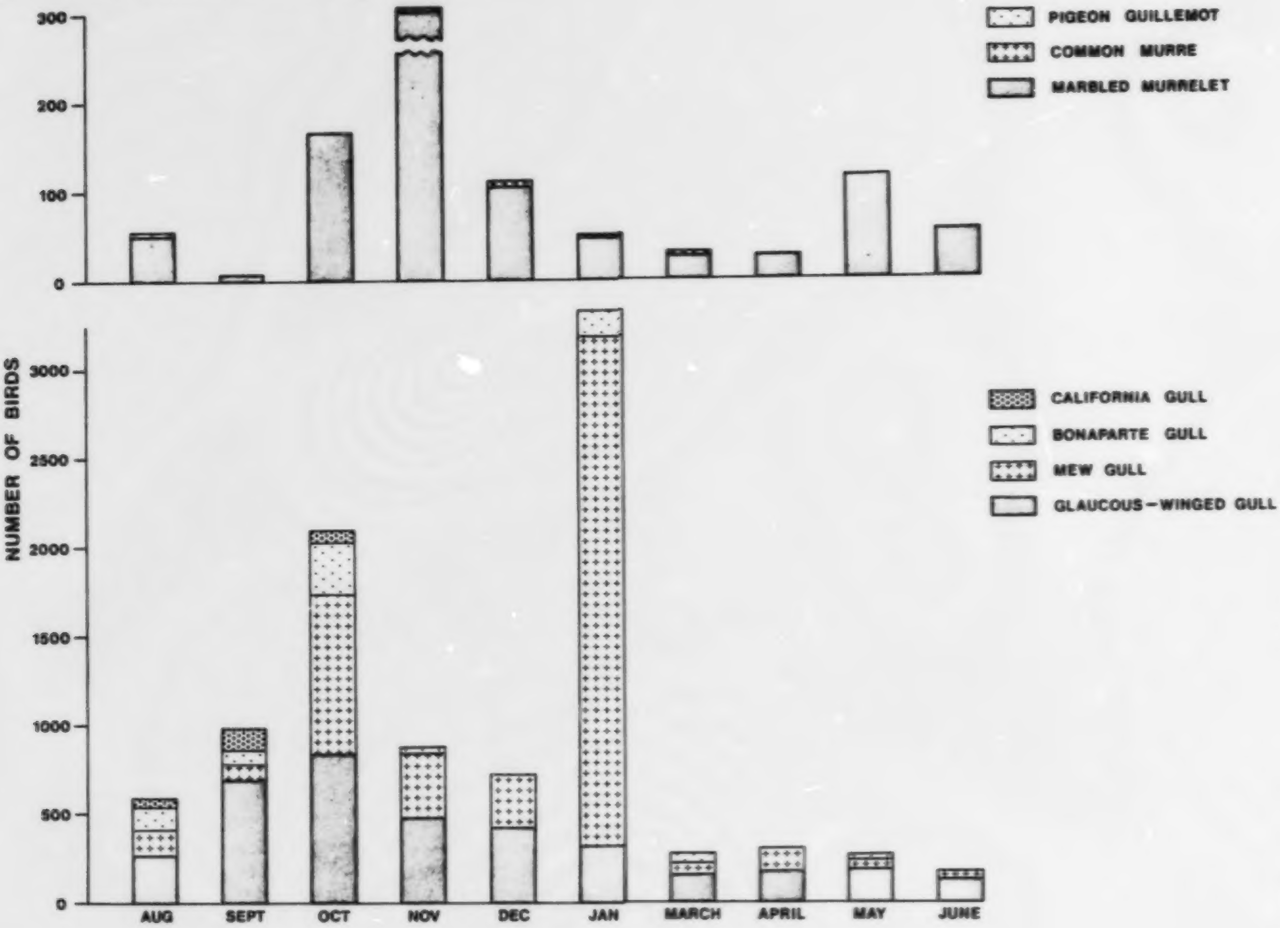


Table 2
Comparison of adult and immature Glaucous-winged Gulls observed in Jervis Inlet, August 1986 – June 1987

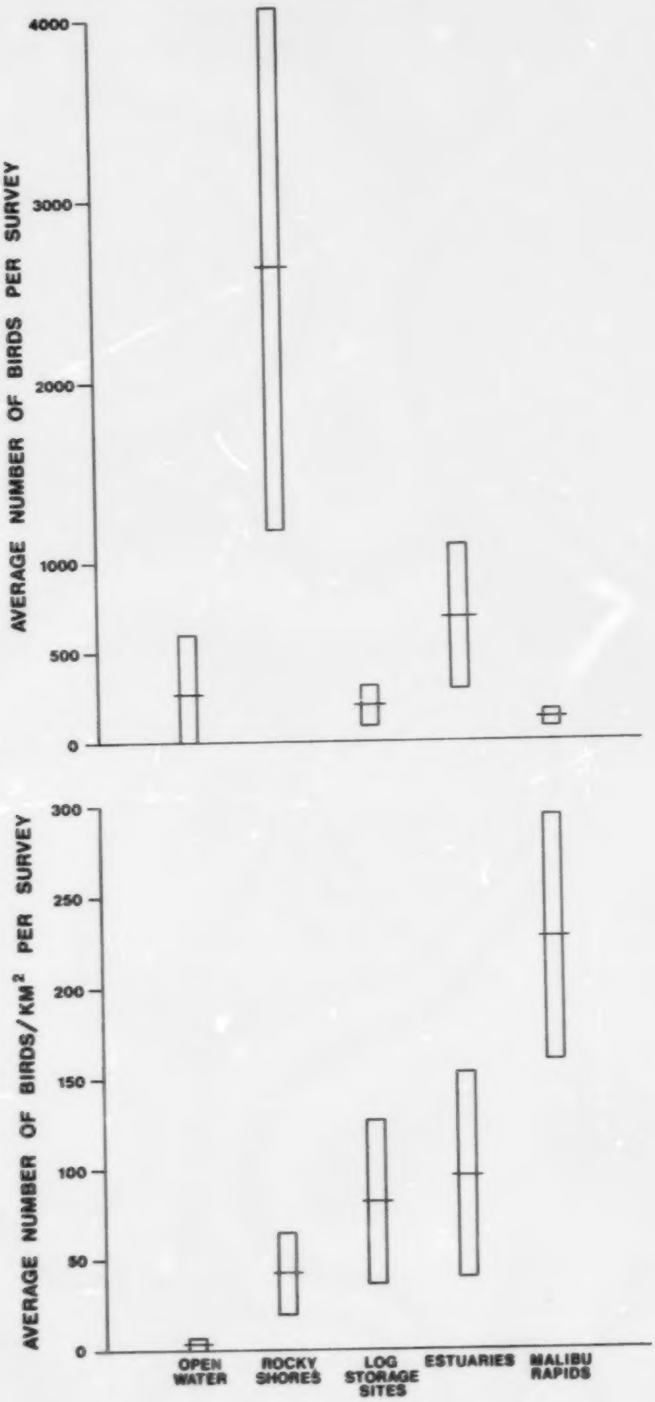
	No. of birds			
Month	**Adults**	**Immatures**	**Total**	**% immatures of total**
August	168	94	262	35.9
September	492	188[a]	680	27.6
October	570	265	835	31.7
November	295	184	479	38.4
December	325	97	422	23.0
January	244	71	315	22.5
March	117	38	155	24.5
April	92	76	168	45.2
May	115	58	173	33.5
June	82	57	139	41.0
Mean ± SD	**250.0 ± 171.4**	**112.8 ± 74.0**	**362.8 ± 240.4**	**32.3 ± 7.9**

[a] 84% of immatures were 1986 fledglings.

Table 3
Extent of different water habitat types (km^2) in Jervis Inlet, as measured from hydrographic chart No. 3514

Habitat type	**Queens Reach**	**Princess Royal Reach**	**Prince of Wales Reach**	**Total of Jervis Inlet**
Open water	27.48	33.31	43.49	104.28
Rocky shore	17.56	18.92	26.08	62.56
Estuary	1.98	2.95	2.29	7.22
Log storage site	0.75	0	1.69	2.44
Malibu Rapids	0.55	0	0	0.55
Total km^2	**48.32**	**55.18**	**73.55**	**177.05**

Figure 7
Overall and average numbers and densities of birds per survey in five different habitats of Jervis Inlet, August 1986 – June 1987. Horizontal lines indicate means, and rectangles 95% confidence intervals.



in winter are the Barrow's Goldeneyes and Surf Scoters (Vermeer 1981; Vermeer *et al.* 1983). Furthermore, they support observations by Vermeer (1983) and Vermeer and Bourne (1984) that those ducks are the most abundant of all birds along steep rock walls of fjords. Although rocky shores—at least for Barrow's Goldeneyes—may not be preferred feeding habitat, these two species may have been attracted to the presence of blue mussels (*Mytilus edulis*), which are attached to the fjord walls. Blue mussels are an important food of Barrow's Goldeneyes and Surf Scoters in fjords (Vermeer 1981).

Higher densities of Barrow's Goldeneyes and Surf Scoters were observed in Queens and Princess Royal reaches than in Prince of Wales Reach. Queens and Princess Royal reaches have less saline surface waters than does Prince of Wales Reach, which is nearer the mouth of Jervis Inlet (Pickard 1961). Barrow's Goldeneyes and Surf Scoters may forage on mussels in less saline habitats of Jervis to avoid salt stress. Salinity apparently is an important habitat barrier in mussel-feeding ducks (Nyström and Pehrsson 1988). The ducks swallow mussels whole with seawater locked between valves. To excrete salt, the net energy balance of the ducks is reduced (Schmidt-Nielsen and King 1964; Peaker and Linzell 1975; Skadhauge 1981).

Precipitation influences salinity of surface waters and, consequently, the choice of duck feeding habitat. August and September are relatively dry months, whereas most of the annual precipitation on the BC coast occurs from late October through March. The observed and progressive movement of Barrow's Goldeneyes and Surf Scoters from Queens Reach (August through October) into Princess Royal Reach (November and December) and upper Prince of Wales Reach (December through March) may relate to increasing freshwater runoff and decreasing salinity in surface waters. During heavy rainfall in November 1977, I observed that many Barrow's Goldeneyes, mostly females, fed below cliff faces over which waters cascaded into Bute and Jervis inlets. The fact that female Barrow's Goldeneyes, which are smaller than male goldeneyes or both sexes of Surf Scoters (Vermeer 1981), fed chiefly below fresh waterfalls is interesting. Nyström and Pehrsson (1988) observed that salt intake is higher in smaller duck species given equal conditions of salinity and equal size of mussels being consumed.

7.2. The importance of tidally active areas

Malibu Rapids makes up such a small fraction (0.3%) of the overall habitat of Jervis Inlet that it may have been considered relatively unimportant had it not been for the high densities of Glaucous-winged and California gulls, Barrow's Goldeneyes, Surf Scoters, Bufflehead, and Pelagic and Double-crested cormorants there (Table 5). California and Glaucous-winged gulls were seen feeding at the exposed intertidal at the foot of the rapids. As there was an established lodge at the rapids, the gulls may have also been attracted to the site by people feeding them. No upwelling was observed at the rapids, which may explain the relatively low densities of Bonaparte's and Mew gulls (Table 4), which are known plankton feeders in areas of tidal upwelling (Vermeer *et al.* 1987*a*). Bonaparte's and Mew gulls, however, were seen feeding in large numbers on euphausiids at Sechelt Rapids in April. As no Bonaparte's Gulls and much smaller numbers of Mew Gulls were observed in Jervis Inlet in April, the presence of euphausiids at Sechelt Rapids may have drawn the gulls away from Jervis Inlet. Marbled Murrelets also had relatively low densities at Malibu Rapids but were numerous at certain times between Egmont and Egmont Point, downstream of Sechelt Rapids. The murrelets may have been feeding on euphausiids or small fishes at Sechelt Rapids.

7.3. Bird utilization of estuaries and log storage sites

Swans, geese, and dabbling ducks were mostly

Table 4
Statistical comparisons of bird densities in different habitats of Jervis Inlet with Kruskall-Wallis and nonparametric multiple range tests

	Mean ranks[a]					
Species	**Open water**	**Rocky shores**	**Estuaries**	**Log storage sites**	**Malibu Rapids**	**Kruskall-Wallis (chi-square)[b]**
All species	7.1	20.6	28.8	27.2	43.8	33.5
Barrow's Goldeneye	5.1	19.9	19.0	23.0	23.0	14.8
Surf Scoter	8.9	24.9	19.9	11.9	24.6	14.4
Glaucous-winged Gull	5.8	17.4	28.8	30.1	44.4	40.2

[a] Mean ranks joined by solid lines are not significant.
[b] Significant ($\alpha = 0.05$).

Table 5
Bird densities for the most common bird species observed in different habitats in Jervis Inlet (higher densities underlined)

			Average no. of birds km^{-2}					
Species	**Period observed[a]**	**n[b]**	**Open water**	**Rocky shores**	**Estuaries**	**Log storage sites**	**Malibu Rapids**	**All habitats**
Common Loon	August–June	10	0.01	0.15	0.72	0.20	0.72	0.09
Red-necked Grebe	September–May	8	0.03	0.32	0.68	3.79	1.36	0.22
Horned Grebe	September–May	8	0.006	0.37	1.14	1.84	0.97	0.20
Western Grebe	October–December, May	4	0.02	0.03	1.70	0.10	0	0.11
Pelagic Cormorant	August–May	9	0.02	0.35	0.57	1.33	11.09	0.21
Double-crested Cormorant	September–May	8	0.02	0.23	1.14	1.79	7.05	0.18
Mallard	October–May	7	0	0.05	8.59	1.23	0	0.39
American Wigeon	October–April	6	0	0.02	2.95	0	0	0.13
Bufflehead	November–May	6	0	0.07	5.49	0	16.36	0.30
Common Goldeneye	November–May	6	0	0.03	4.39	0.14	1.21	0.19
Barrow's Goldeneye	October–May	7	0.11	21.62	21.82	27.58	52.72	9.13
Surf Scoter	October–May	7	0.26	27.25	13.46	4.04	57.67	9.47
Common Merganser	August–June	10	0.02	0.73	3.39	1.07	1.64	0.42
Glaucous-winged Gull	August–June	10	0.20	2.58	9.86	21.64	103.27	2.05
Mew Gull	August–May	9	1.57	1.21	35.80	18.17	5.25	3.08
California Gull	August–October	3	0.03	0.11	1.89	16.80	29.09	0.45
Bonaparte's Gull	August–November, January, March	5	0.30	0.79	3.25	6.28	0.90	0.67
Marbled Murrelet	August–June	10	0.27	0.92	2.49	2.42	1.09	0.63

[a] Period when most commonly present.
[b] Number of surveys.

restricted to the small estuaries in Jervis Inlet, which is not surprising, as these birds do not dive for their food and are known to feed in shallow waters. Other habitats in Jervis Inlet are too deep for this group of birds to feed.

Two diving ducks, the Bufflehead and Common Goldeneye, also occurred in relatively high densities in the estuaries (Table 5). Those species are known to feed extensively on snails and crustaceans (Vermeer 1982). Snails and crustaceans may be more abundant and available to the ducks in estuaries than along fjord walls. The Barrow's Goldeneye had higher densities at log storage sites than any other species (Table 5). Habitat segregation between Common and Barrow's goldeneyes was also observed at Howe Sound—the former was most abundant in the head estuary, whereas the latter predominated along rocky shores and log storage sites (Vermeer 1982).

Western Grebes occurred mostly in estuaries, whereas Horned and Red-necked grebes were found in their highest density at log storage sites. Some habitat segregation between Western Grebes on one hand and Horned and Red-necked grebes on the other may be related to dietary differences. Western Grebes eat mostly fishes, whereas Horned Grebes are known to eat much shrimp (Vermeer and Ydenberg, this publication). Shrimp and other crustaceans may be associated with log storage sites. Little is known of the diet of Red-necked Grebes.

Relatively high densities at log storage sites were observed for all gull species (Table 5). The gulls were chiefly observed loafing or resting on the logs, but grebes and goldeneyes occurred on the water surface and were seen diving.

7.4. Comparison of bird composition in Jervis Inlet and the Strait of Georgia

Bird surveys in the Strait of Georgia show that the strait, like Jervis Inlet, is mostly utilized by birds from autumn to spring (Vermeer 1983; Vermeer *et al.* 1983), but bird composition differs from that of Jervis Inlet in that many species that are common or numerous in the strait are scarce or absent in the inlet. For example, Pacific Loons, Western Grebes, Brandt's Cormorants (*Phalacrocorax penicillatus*), and Common Murres are either relatively scarce or absent in Jervis Inlet, but common or numerous in the Strait of Georgia (Vermeer 1983; Vermeer *et al.* 1983). Pacific herring (*Clupea harengus*) is an important food in the diet of those species, and the birds follow the

Figure 8
Average numbers and densities of Barrow's Goldeneyes, Surf Scoters, and Glaucous-winged Gulls per survey in Jervis Inlet, October 1986 – May 1987. Horizontal lines indicate means, and rectangles 95% confidence intervals.

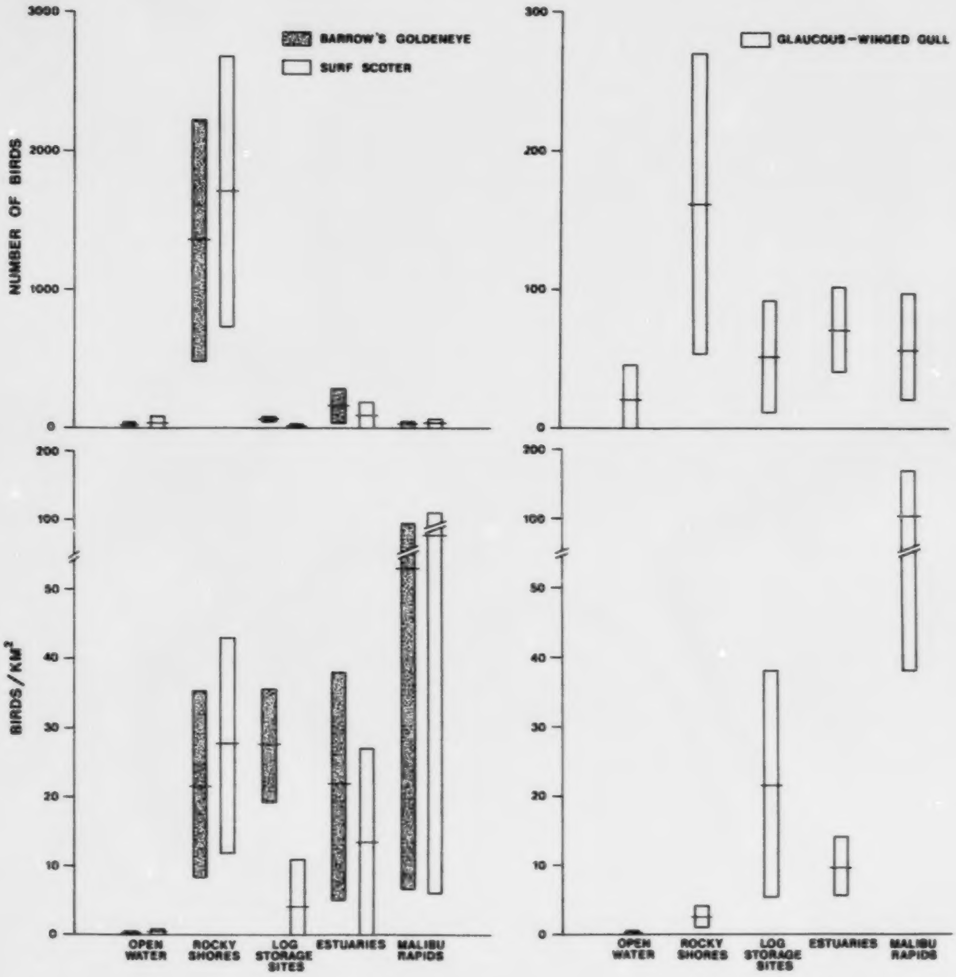


Table 6
Comparison of densities of Barrow's Goldeneyes and Surf Scoters in Queens, Princess Royal, and Prince of Wales reaches, Jervis Inlet, August 1986 – June 1987

	No. of birds km^{-2}					
	Barrow's Goldeneye			Surf Scoter		
Month	Queens	Royal	Wales	Queens	Royal	Wales
August	0	0	0	1.18	0.36	0
September	0.08	0.02	0	6.56	0.05	0
October	2.69	0.24	0.03	49.92	6.43	0
November	14.65	18.14	5.78	8.84	37.50	0.12
December	18.13	17.20	11.15	14.40	30.35	2.04
January	15.00	7.19	6.70	26.24	4.64	10.88
March	9.21	30.23	7.38	4.76	9.13	5.47
April	13.12	11.42	3.47	9.06	1.18	0.30
May	6.97	2.45	0.39	18.69	4.08	2.03
June	0.08	0	0	0.29	0	0
Average density ± SD	**7.99 ± 7.01**	**8.69 ± 10.39**	**3.49 ± 4.05**	**13.99 ± 14.93**	**9.37 ± 13.39**	**2.08 ± 3.55**

movements of herring until they spawn in sheltered and shallow waters of the strait (Vermeer and Ydenberg, this publication). After the spawning of herring, the birds depart from the strait. Pacific herring do not usually spawn in deep fjord waters.

The main water body of Jervis Inlet is too deep for several diving species that forage on or near the bottom substrate. For example, White-winged Scoters and Pigeon Guillemots are scarce in Jervis Inlet, but numerous in the Strait of Georgia (Vermeer 1983; Vermeer *et al.* 1983).

White-winged Scoters feed mostly on clams inhabiting gravel and mud substrates (Vermeer and Bourne 1984), whereas Pigeon Guillemots chiefly feed epibenthically (Drent 1965; Follett and Ainley 1976; Krasnow and Sanger 1986).

The California Gull was one species that seemed to be more common in Jervis Inlet than in the Strait of Georgia in late summer and early autumn. The relative abundance of California Gulls compared with that of Glaucous-winged Gulls in the strait, however, has not been very well documented, and California Gulls may have been included in counts with Glaucous-winged Gulls during bird surveys there. California Gulls were also common in Saanich Inlet, a Vancouver Island fjord, during August, September, and October 1986 (Morgan, this publication). Perhaps Jervis Inlet and other fjords are major passageways for the dispersion of these gulls from their breeding colonies in the Canadian Prairie provinces to the coast. Although not uncommon in the Strait of Georgia, most California Gulls spend little time there compared with the southwest coast of Vancouver Island, where they outnumber Glaucous-winged Gulls in September and are associated with the offshore fishing fleet (Vermeer *et al.* 1987*b*).

7.5. Recommendations for further study

The 1-d monthly surveys provide a first glimpse of the composition, seasonal variation in numbers, and different habitat utilization by bird species in Jervis Inlet. Little is known about the daily variation in numbers and species, movements, and diet of birds in BC mainland fjords. Some of these information gaps could be addressed by the following investigations:

(1) The daily variation in bird composition, numbers, and movements needs to be investigated during one whole month, preferably during the high utilization months of November–January.

(2) The feeding ecology of the whole marine bird community of Jervis Inlet should be investigated from autumn until spring.

(3) The distribution of the main prey organisms (particularly blue mussels) of birds in Jervis Inlet should be mapped.

(4) The distribution of birds and that of their prey organisms should be compared between a fjord with mostly glacial runoff (e.g., Bute Inlet, Howe Sound) and one with mostly nonglacial runoff (e.g., Jervis Inlet).

(5) Because aquaculture is becoming rapidly established at estuaries, mouths of creeks, and waterfalls throughout Jervis Inlet, interactions between marine birds and aquaculture operations should be investigated.

8. Acknowledgements

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Marine birds of Saanich Inlet, a Vancouver Island fjord entering the Strait of Georgia

Ken H. Morgan

1. Abstract

Marine birds were surveyed in Saanich Inlet from 11 March to 15 December 1986. The density of birds ranged from 7.6 birds per square kilometre in July to 114.5 birds per square kilometre in December. Averaged over the entire study period, Western Grebe (*Aechmophorus occidentalis*) and Glaucous-winged Gull (*Larus glaucescens*) had the highest densities. In descending order, Bufflehead (*Bucephala albeola*), Red-breasted Merganser (*Mergus serrator*), Barrow's Goldeneye (*Bucephala islandica*), White-winged Scoter (*Melanitta fusca*), and Surf Scoter (*M. perspicillata*) were the most abundant ducks.

Four habitat types were recognized in the inlet: open waters (42.6 km^2), rocky shores (11.2 km^2), shallow bays (7.9 km^2), and waters off extensive beaches (2.8 km^2). There were significantly more birds in shallow bays than along rocky shores. Most species of birds were at their peak density in shallow bays, whereas the lowest densities usually occurred in stretches of open water. The proportion of birds in shallow bays was lowest at high tide.

2. Résumé

Les oiseaux de mer présents dans l'inlet Saanich ont été observés du 11 mars au 15 décembre 1986. La densité fluctuait entre 7,6 oiseaux par kilomètre carré en juillet et 114,5 par kilomètre carré en décembre. Les espèces dont la densité moyenne pour toute la période d'étude était la plus élevée sont le Grèbe de l'Ouest (*Aechmophorus occidentalis*) et le Goéland à ailes grises (*Larus glaucescens*). Chez les canards, les espèces les plus abondantes étaient, par ordre décroissant, le Petit Garrot (*Bucephala albeola*), le Bec-scie à poitrine rousse (*Mergus serrator*), le Garrot de Barrow (*Bucephala islandica*), la Macreuse à ailes blanches (*Melanitta fusca*) et la Macreuse à front blanc (*M. perspicillata*).

Quatre types d'habitat ont été reconnus : les eaux libres (42,6 km^2), les rivages rocheux (11,2 km^2), les baies peu profondes (7,9 km^2) et les eaux devant les plages étendues (2,8 km^2). On a observé nettement plus d'oiseaux dans les baies peu profondes que sur les rivages rocheux. Pour la plupart des espèces, la densité était maximale dans les baies peu profondes et elle était ordinairement minimale dans les zones d'eau libre. Dans les baies peu profondes, la densité était plus faible à marée haute.

3. Introduction

Aerial surveys of the southeast coast of Vancouver Island and the Gulf Islands indicated a large, diverse population of marine birds (Vermeer *et al.* 1983). Saanich Inlet, the largest fjord on the east coast of Vancouver Island, was not censused by Vermeer *et al.* (1983). I surveyed the marine birds of Saanich Inlet for approximately nine months in 1986 to record the spatial and temporal patterns of distribution and abundance.

4. Study area

The biological, physical, and geochemical characteristics of Saanich Inlet have been well described by Herlinveaux (1962) and Juniper and Brinkhurst (1984) and are briefly summarized here. The inlet is a 24-km-long embayment oriented in a north–south direction (Fig. 1). The deepest part of the inlet (228 m) occurs off Sheppard Point, whereas there is a shallow sill of 75 m at the mouth. There is no significant source of fresh water at the head or along the length of the inlet. Instead, most fresh water entering Saanich Inlet comes from the Cowichan River to the north. Peak discharge from the Cowichan River occurs in December, and the minimum normally occurs in August. The lack of significant freshwater discharge, the presence of the sill, and the narrow, deep morphology severely restrict the circulation of water. Consequently, for much of the year, the bottom waters are anoxic.

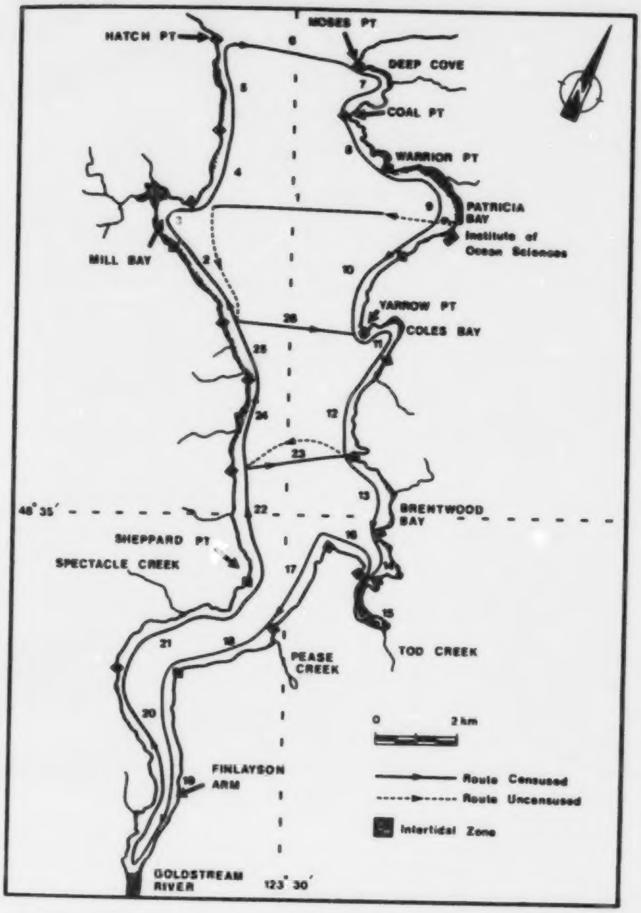
Most fjords are bordered by more or less coherent, vertical rock walls. In contrast, steep rock faces account for less than 40% of the perimeter of Saanich Inlet. North of Sheppard Point and Brentwood Bay, the shoreline is primarily either an accumulation of boulders and small rock or a series of sand and cobble beaches.

5. Methods

Saanich Inlet was surveyed approximately every two weeks from 11 March to 15 December 1986. Each survey was conducted by one or two observers, plus a recorder, aboard a small launch. The launch paralleled the coastline, roughly 150 m offshore, at a speed of 20–30 km·h^{-1}. Whenever a large concentration of birds was encountered, the boat was stopped. All birds observed within approximately 150 m of either side of the launch were tallied.

The perimeter of the inlet was divided into 22 transects according to shoreline features. Four open-water transects crossing the inlet were also surveyed. Birds in each transect were counted separately. The length and area of each transect, as well as the total inlet area, were measured using a planimeter and a 1:40 000 Canadian Hydrographic Service chart (No. 3310). Two methods were used to calculate bird density (birds km^{-2}):

Figure 1
Saanich Inlet, showing the survey route and the location of each transect. Transect numbers are shown along the survey routes.



(1) the total number of birds divided by the area surveyed ($28.7\ km^2$); and
(2) the total number of birds divided by the total area of Saanich Inlet ($64.5\ km^2$).

Within the inlet, four broad habitat types were recognized:

(1) shallow bays;
(2) areas (other than bays) with extensive beaches;
(3) rocky shorelines including steep fjord walls; and
(4) open water.

Although few transects were characterized exclusively by a single type of habitat, each transect was categorized by its dominant habitat type. During the surveys, the time was noted at the beginning of each transect to determine the tidal level for each transect. The proportion of birds within each habitat type during a given tidal interval (out of the total number present in the inlet during that interval) was regressed against the midpoint of each tidal interval, using the Product-moment Correlation Coefficient (Zar 1974).

6. Results and discussion

6.1. Species composition and seasonal changes

In total, 48 species of marine birds were identified during this study. The highest total population, number of pecies, and density occurred in November and December, nd the lowest during June and July (Table 1). The aver- ge monthly populations and number of species included every bird species observed. Some species were rarely encountered and do not appear in Tables 3–8. Consequently, the average monthly populations presented in Table 3 are greater than the sum of the monthly populations listed in Tables 3–8.

Table 1
Average population, average number of species, and average density of all marine birds observed in Saanich Inlet, by month

Month	Population	No. of species	Density No. 1[a]	Density No. 2[b]
March	3990.5	33.5	139.2	61.9
April	4785.5	33.5	166.9	74.2
May	1336.0	24.5	46.5	20.7
June	610.0	14.0	21.3	9.5
July	491.0	13.0	17.1	7.6
August	1000.0	20.0	34.9	15.5
September	1218.0	20.0	42.5	18.9
October	4953.0	27.0	172.8	76.8
November	5917.5	36.5	206.4	91.8
December	7386.0	36.0	257.6	114.5

[a] Density No. 1 = number of birds per square kilometre (surveyed area only).
[b] Density No. 2 = number of birds per square kilometre (entire area of Saanich Inlet).

The seasonal changes in the population and diversity of species primarily reflected the two peak migration periods (March–April and November–December) and the breeding season activities (May through September). Manuwal *et al.* (1979) and Vermeer (Part 5, this publication) observed similar trends in the Strait of Juan de Fuca and in Jervis Inlet, respectively.

Each survey of Saanich Inlet covered approximately 45% of the total surface area. It is therefore unlikely that every bird within the inlet was counted. However, to compare the results of this study with densities determined for the total area of Jervis Inlet (Vermeer, Part 5, this publication), Table 1 presents both the density based on total surface area and the density based on the surveyed area only. Saanich Inlet supported an overall average bird density that was at least twice as large as that of Jervis Inlet. This difference was likely due to a number of factors, including the lack of shallow bays and extensive intertidal areas in, and the more northern position of, Jervis Inlet.

Vermeer *et al.* (1983) reported densities as high as 255 birds per kilometre in surveys of the east coast of Vancouver Island and the adjacent Gulf Islands during March. This greatly exceeds the maximum density found in Saanich Inlet ($257.6\ birds\ km^{-2} = 93.7\ birds\ km^{-1}$). Vermeer (1981) observed that large flocks of loons, grebes, cormorants, gulls, and ducks had been attracted to the spawning grounds of Pacific herring (*Clupea harengus pallasi*). Herring have spawned in Saanich Inlet in the past, but no spawning populations occur there now (Woods and Shaw 1981). The absence of this very important prey species may account for much of the differences in bird densities observed in this study and that by Vermeer *et al.* (1983).

Of the six major bird categories in Saanich Inlet, waterfowl dominated from March through May and again in November and December (Table 2). Although 21 species were identified, seven species accounted for more than 90% of all waterfowl. Bufflehead (*Bucephala albeola*) were the most abundant waterfowl, especially during March, April, and November (Table 3). Vermeer (1982) observed that from mid-October to May, Bufflehead were the most numerous of the *Bucephala* species in sheltered waters of southern British Columbia.

Table 2
Average monthly percentages (of total inlet population) of the six major categories of birds

Month	Loons	Grebes	Cormorants	Gulls	Waterfowl	Alcids
March	0.96	14.07	3.64	18.50	62.49	0.34
April	1.38	38.79	3.11	13.51	42.79	0.42
May	1.06	2.55	10.30	39.20	45.86	1.03
June	0.84	0.00	22.73	68.52	6.23	1.68
July	0.43	0.00	13.62	78.72	6.38	0.85
August	0.31	3.26	4.93	78.07	7.87	5.56
September	1.85	15.23	7.14	60.73	11.09	3.96
October	5.36	62.63	2.93	15.53	12.41	1.14
November	1.11	25.40	2.94	17.88	51.50	1.17
December	1.73	35.42	2.19	17.97	40.22	2.47

Table 3
Average monthly populations of the seven most numerous species of waterfowl in Saanich Inlet[a]

Month	American Wigeon	White-winged Scoter	Surf Scoter	Barrow's Goldeneye	Common Goldeneye	Bufflehead	Red-breasted Merganser
March	149.5	275.0	219.0	367.0	375.0	509.0	365.5
April	17.5	366.0	273.5	249.5	106.5	466.0	297.0
May	0.0	197.5	166.5	53.5	19.0	61.5	45.5
June	0.0	3.5	1.0	0.0	0.0	0.0	0.0
July	0.0	0.5	0.0	0.0	0.5	0.0	0.0
August	0.0	0.0	21.5	0.5	0.5	0.0	0.0
September	0.0	47.0	68.0	0.0	0.0	0.0	0.5
October	51.5	137.5	199.5	3.0	0.0	21.5	153.0
November	219.5	188.0	241.5	542.0	315.5	737.0	586.0
December	213.0	215.0	224.0	334.0	468.0	592.0	638.0

[a] Values listed are the total monthly population divided by the number of surveys. An additional 14 species occurred in the inlet in small numbers.

In Saanich Inlet, the next most abundant waterfowl was the Red-breasted Merganser (*Mergus serrator*). Its numbers peaked in November and December. Vermeer *et al.* (1983) stated that this was the most common merganser along the BC coast.

The overall total populations of White-winged Scoter (*Melanitta fusca*) and Surf Scoter (*M. perspicillata*) were extremely similar—2686 and 2605, respectively. Whereas White-winged Scoters outnumbered Surf Scoters by approximately 30% in March and April, the reverse occurred from September through December. This is in sharp contrast to what Vermeer (Part 5, this publication) observed in Jervis Inlet.

Barrow's Goldeneye (*Bucephala islandica*) and Common Goldeneye (*B. clangula*) were at their highest densities during March, November, and December. Although Vermeer (1982) found that Barrow's Goldeneye predominated in mainland fjords, he speculated that Common Goldeneye were more numerous along southeast Vancouver Island. The results from this study do not entirely support Vermeer (1982), as Common Goldeneye were the least abundant of the three *Bucephala* species.

American Wigeon (*Anas americana*) was the only relatively abundant dabbling duck in Saanich Inlet. It was most numerous in November and December. This species congregates near streams and estuaries in the Strait of Georgia from October through December (Vermeer *et al.* 1983).

From June through September, gulls were the most numerous bird group (Table 2). Seven species of gull were identified in the inlet. However, Glaucous-winged Gulls (*Larus glaucescens*) were by far the most common, accounting for more than 75% of all gulls (Table 4). Approximately 71% (range 65.3–77.6) of all Glaucous-winged Gulls were adults.

Mew Gulls (*Larus canus*) were the second most common species of gull. Although they were observed in every month but July, they were most abundant during March and April and October through December. Mew Gulls overwinter in southern British Columbia and are common along the Strait of Georgia during spring and fall (Vermeer *et al.* 1983, 1987).

Bonaparte's (*Larus philadelphia*) and California (*L. californicus*) gulls were most abundant from August through October. Both species nest inland and pass through the Strait of Georgia in their spring and fall migrations (Vermeer *et al.* 1983; Vermeer and Devito 1987). Thayer's (*L. thayeri*), Herring (*L. argentatus*), and Western (*L. occidentalis*) gulls were infrequently encountered in this study, primarily in the spring and early winter.

Pelagic (*Phalacrocorax pelagicus*) and Double-crested (*P. auritus*) cormorants were present throughout the entire study. Pelagic cormorants were most numerous during March and December, whereas the number of Double-crested Cormorants peaked in June (Table 5). Both species nest nearby in the Gulf Islands and the Strait of Georgia (Vermeer and Morgan, this publication). Brandt's Cormorants (*P. penicillatus*) were rarely observed.

Grebes were abundant in April and again from October through December (Table 6). Five species were identified, but Western (*Aechmophorus occidentalis*), Horned (*Podiceps auritus*), and Red-necked (*P. grisegena*) grebes accounted for over 99% of all grebes. Vermeer *et al.* (1983) noted that Western Grebes wintered by the tens of thousands in the Gulf Islands. This species normally reaches the Strait of Georgia from its interior nesting colonies in the early fall. Its numbers continue to rise throughout the winter until the end of the spawning of herring in March or April (Vermeer 1983). Horned and Red-necked grebes were most numerous from October through December. Eared Grebe (*P. nigricollis*) was relatively common only in March and April, and Pied-billed Grebe (*Podilymbus podiceps*) was rarely encountered.

Table 4
Average monthly populations of gull species in Saanich Inlet[a]

Month	Glaucous-winged Gull	Mew Gull	Bonaparte's Gull	California Gull	Thayer's Gull	Herring Gull	Western Gull[b]
March	531.5	198.0	0.0	2.5	2.5	0.0	0.0
April	666.0	163.0	7.5	21.0	0.5	2.0	0.0
May	510.5	2.0	2.0	0.5	0.0	0.0	0.5
June	404.0	0.5	2.0	0.0	0.0	0.0	0.0
July	366.0	0.0	0.0	4.0	0.0	0.0	0.5
August	316.0	75.0	264.0	89.0	0.0	0.0	0.0
September	440.5	36.5	135.0	93.5	0.0	0.0	0.5
October	492.0	126.0	63.5	84.0	0.0	0.0	0.0
November	824.5	219.0	1.0	0.0	2.5	2.5	5.0
December	1170.0	139.0	0.0	0.0	5.0	3.0	3.0

[a] Values listed are the total monthly population divided by the number of surveys.
[b] Includes Western × Glaucous-winged gull hybrids.

Table 5
Average monthly populations of cormorant species in Saanich Inlet[a]

Month	Pelagic Cormorant	Double-crested Cormorant	Brandt's Cormorant
March	101.5	42.5	0.5
April	89.5	50.5	0.5
May	60.5	72.5	0.0
June	40.0	95.0	0.0
July	33.0	31.0	0.0
August	12.5	34.5	0.0
September	34.0	49.0	0.0
October	70.5	73.5	0.5
November	95.5	75.5	3.0
December	112.0	49.0	0.0

[a] Values listed are the total population divided by the number of surveys.

Table 6
Average monthly populations of grebe species in Saanich Inlet[a]

Month	Western Grebe	Horned Grebe	Red-necked Grebe	Eared Grebe	Pied-billed Grebe
March	310.5	192.0	40.0	14.5	1.5
April	1434.5	243.0	45.5	28.5	0.0
May	3.5	18.5	8.0	3.5	0.0
June	0.0	0.0	0.0	0.0	0.0
July	0.0	0.0	0.0	0.0	0.0
August	0.0	1.0	29.5	0.0	0.0
September	88.0	57.5	29.5	0.0	2.0
October	2613.5	342.0	131.5	0.0	0.0
November	1059.5	351.5	86.5	0.5	0.5
December	2050.0	414.0	144.0	0.0	0.0

[a] Values listed are the total population divided by the number of surveys.

The two least numerous groups of birds were the loons and the alcids. Although four species of loons were found in Saanich Inlet, only Common (*Gavia immer*) and Pacific (*G. pacifica*) loons were relatively abundant (Table 7). Common Loons normally outnumbered Pacific Loons except in early October, when a single raft of 350 Pacific Loons was present between Patricia Bay and Yarrow Point (Fig. 1). Red-throated (*G. stellata*) and Yellow-billed (*G. adamsii*) loons were rare visitors to the inlet.

Five species of alcids were encountered, with Common Murre (*Uria aalge*) and Marbled Murrelet (*Brachyramphus marmoratus*) being relatively abundant in November and December (Table 8). Rhinoceros Auklets (*Cerorhinca monocerata*) also were common only during November and December. A single Ancient Murrelet (*Synthliboramphus antiquus*) was observed in November.

6.2. Bird densities and habitat relationships

Open waters and rocky shores were the dominant habitat types in Saanich Inlet, whereas shallow bays and waters off extensive beaches accounted for less than 17% of the total surface area (Table 9). In contrast to the proportions of surface area by habitat type, shallow bays supported significantly higher bird densities than did rocky shorelines (Table 10).

Table 11 presents the overall average densities of the 23 most commonly observed bird species in Saanich Inlet. Based on highest average density by habitat type, Western Grebe, Pacific Loon, and Glaucous-winged Gull were the three most numerous species in open waters. Similarly, Glaucous-winged Gull, Western Grebe, and White-winged Scoter were the three most abundant species in shallow bays. Along extensive beach habitats, Glaucous-winged Gull, California Gull, and Barrow's Goldeneye were most common, and Glaucous-winged Gull, Red-breasted Merganser, and Barrow's Goldeneye had the highest densities along rocky shores.

By comparing species densities between habitat types, Table 11 shows that Pacific Loon, Western Grebe, and Common Murre were most numerous in open waters, especially between Patricia Bay and Mill Bay (Fig. 1). These three species normally feed either in open waters

Table 7
Average monthly populations of loon species in Saanich Inlet[a]

Month	Common Loon	Pacific Loon	Red-throated Loon	Yellow-billed Loon
March	32.5	4.0	1.5	0.0
April	48.5	14.0	0.0	0.0
May	7.0	6.0	1.0	0.0
June	4.0	1.0	0.0	0.0
July	0.0	2.0	0.0	0.0
August	3.0	0.0	0.0	0.0
September	18.5	3.0	0.0	0.0
October	42.5	221.5	0.0	0.0
November	47.5	17.0	1.0	0.0
December	55.0	69.0	1.0	2.0

[a] Values listed are the total population divided by the number of surveys.

Table 8
Average monthly populations of alcid species in Saanich Inlet[a]

Month	Common Murre	Marbled Murrelet	Pigeon Guillemot	Rhinoceros Auklet	Ancient Murrelet
March	8.0	0.0	5.5	0.0	0.0
April	0.0	12.5	6.0	0.5	0.0
May	0.0	9.5	4.0	0.0	0.0
June	0.0	3.0	7.0	0.0	0.0
July	0.0	1.0	3.0	0.0	0.0
August	25.0	15.5	11.0	1.5	0.0
September	31.0	3.0	12.0	0.0	0.0
October	27.0	14.0	11.5	3.5	0.0
November	41.5	16.0	2.5	8.0	0.5
December	110.0	52.0	6.0	13.0	0.0

[a] Values listed are the total population divided by the number of surveys.

(especially over reefs) or in the entrances of bays and estuaries (Angell and Balcomb 1982; Trethewey 1985). Large rafts of Western Grebes (up to 2000 birds) greatly inflated the average bird densities calculated for Saanich Inlet open water (Table 10). Open waters had the lowest density of birds in Jervis Inlet (Vermeer, Part 5, this publication), whereas rocky shorelines supported the fewest birds in Saanich Inlet. Unlike the situation in Saanich Inlet, Western Grebes were never abundant in Jervis Inlet. By excluding Western Grebes from the calculation, the average open-water density of Saanich Inlet becomes 5.7 birds per kilometre per survey (the lowest of the four habitat types).

The majority (13/23) of the species listed in Table 11 reached their peak densities in shallow bays. A preference for foraging in shallow bays has been well documented for all but two of these species (Munro and Clemens 1932; Bent 1962; Brattstrom 1965; Erskine 1972; Morrison *et al.* 1978; Manuwal *et al.* 1979; Ainley *et al.* 1981; Forsell and Gould 1981; Stott and Olson 1982; Krasnow and Sanger 1983; Baird 1983; Nysewander 1983*a*, 1983*b*; Sanger 1983; Vermeer 1983; Vermeer *et al.* 1983; Johnson 1984). The two exceptions are Pelagic Cormorant and Surf Scoter. Whereas Dow (1964) stated that Pelagic Cormorants frequently utilized shallow waters, foraging above the intertidal zone, Robertson (1974), Manuwal *et al.* (1979), Ainley *et al.* (1981), and Nysewander (1983*a*) claimed that this species preferred to forage along rocky shores or in the surf beside steep cliffs. Man-made roosts, including log booms, buoys, and docks, are regularly used by Pelagic Cormorants (Manuwal *et al.* 1979). In Saanich Inlet, roosts of this type were most numerous in shallow bays. This may partially explain why the density of Pelagic Cormorants was highest in these habitats. The second highest density of Pelagic Cormorants occurred along rocky shorelines, in agreement with many authors.

Surf Scoters are often very abundant along the steep rock walls of fjords (Vermeer and Levings 1977; Vermeer 1981; Vermeer and Bourne 1984), where they feed primarily upon blue mussels (*Mytilus edulis*). Along the rocky walls of Jervis Inlet, Surf Scoters were the most numerous species of bird (Vermeer, Part 5, this publication). In contrast, along both the Pacific and Atlantic coasts, Surf Scoters have occurred in higher densities in shallow bays than along rocky shores (Grosz and Yocom 1972; Scott-Brown 1976; Manuwal *et al.* 1979; Stott and Olson 1982). In fact, Stott and Olson (1982) reported a decrease in the density of Surf Scoters as the proportion of rocky substrate increased. Molluscs, especially bivalves, make up the bulk of the diet of Surf Scoters, although these birds also frequently take polychaetes, barnacles, crabs, sea urchins, sand dollars, starfish, and small fish (Cottam 1939; Sanger 1983). Shallow bays in Saanich Inlet support a rich and diverse intertidal and subtidal community (Woods and Shaw 1981). Heart cockles (*Clinocardium nuttallii*), bent-nosed (*Macoma nasuta*), butter (*Saxidomus giganteus*), and littleneck (*Protothaca staminea*) clams, plus many species of crabs, snails, and polychaetes were very abundant in the intertidal zone in Patricia Bay (Morgan *et al.* 1987). The highest densities of Surf Scoters in Saanich Inlet occurred in Patricia Bay, followed by Mill Bay and Coles Bay (Fig. 1). In typical fjords, in which shallow bays and estuaries are either scarce or absent, mussels attached to the steep rock faces may provide the only abundant and available supply of food. This could explain the high densities of Surf Scoters observed along the rocky shorelines of Jervis and other fjord-like inlets.

Five species of birds were most abundant in areas with extensive beaches. Along the BC coast, American Wigeon concentrate near streams and estuaries (Vermeer *et al.* 1983), where they feed almost exclusively on plants

Table 9
Extent of water habitat types and percentages of total inlet surface area

Habitat type	Surface area (km^2)	% of total inlet
Open water (1, 6, 23, 26)[a]	42.6	66.0
Shallow bays (3, 7, 9, 11, 13–15)	7.9	12.3
Extensive beaches (2, 5, 24, 25)	2.8	4.3
Rocky shores (4, 8, 10, 12, 16–22)	11.2	17.4

[a] Numbers in parentheses refer to transect number.

Table 10
Average number of birds per survey and average number of birds per kilometre per survey (entire study period)

Habitat type	Average no. of birds/survey	Average no. of birds/km/survey
Open water	189.3 ± 245.4	36.4 ± 47.2
Shallow bays	336.5 ± 240.5	73.2 ± 52.4
Extensive beaches	143.7 ± 13.4	42.6 ± 12.3
Rocky shores	86.6 ± 69.8	21.7 ± 17.5

Note: The average density of birds in shallow bays was significantly different ($P < 0.05$) from the average density along rocky shores (Kruskall-Wallis nonparametric analysis of variance).

Table 11
Average densities (birds km^{-1}) of the 23 most common species of birds, by habitat type[a]

Species	Open water	Shallow bay	Extensive beach	Rocky shore
Pacific Loon	1.29 ± 2.17*	0.31 ± 0.39	0.16 ± 0.12	0.46 ± 0.67
Western Grebe	35.16 ± 46.99*	8.65 ± 14.69	0.30 ± 0.47	0.06 ± 0.06
Common Murre	0.75 ± 0.60*	0.02 ± 0.03	0.02 ± 0.03	0.05 ± 0.08
Common Loon	0.11 ± 0.11	0.69 ± 0.55*	0.39 ± 0.25	0.16 ± 0.14
Horned Grebe	0.09 ± 0.16	4.59 ± 3.97*	1.66 ± 1.46	0.99 ± 0.86
Red-necked Grebe	0.12 ± 0.07	1.41 ± 1.30*	0.56 ± 0.52	0.35 ± 0.28
Double-crested Cormorant	0.16 ± 0.12	1.70 ± 0.65*	0.77 ± 0.47	0.38 ± 0.11
Pelagic Cormorant	0.18 ± 0.12	1.45 ± 0.49*	0.44 ± 0.33	0.76 ± 0.61
White-winged Scoter	0.15 ± 0.10	7.16 ± 7.69*	0.59 ± 0.88	0.66 ± 0.74
Surf Scoter	0.11 ± 0.09	5.81 ± 4.54*	1.33 ± 1.52	0.63 ± 0.67
Common Goldeneye	0.00	2.22 ± 3.79*	0.97 ± 1.67	0.49 ± 0.84
Bufflehead	0.00	5.62 ± 9.36*	1.47 ± 2.55	0.55 ± 0.96
Red-breasted Merganser	0.22 ± 0.23	3.61 ± 4.37*	1.48 ± 1.69	1.22 ± 1.63
Mew Gull	0.15 ± 0.11	2.29 ± 2.54*	1.53 ± 0.68	0.76 ± 0.39
Glaucous-winged Gull	1.04 ± 0.09	14.25 ± 4.27*	8.25 ± 3.64	3.82 ± 0.98
Pigeon Guillemot	0.03 ± 0.02	0.20 ± 0.08*	0.11 ± 0.09	0.08 ± 0.05
American Wigeon	0.03 ± 0.05	0.73 ± 1.19	0.98 ± 0.69*	0.21 ± 0.24
Barrow's Goldeneye	0.00	1.86 ± 3.11	2.19 ± 3.79*	1.10 ± 1.88
Bonaparte's Gull	0.41 ± 0.31	0.99 ± 0.86	1.53 ± 1.79*	0.54 ± 0.57
California Gull	0.14 ± 0.17	0.46 ± 0.39	2.73 ± 2.47*	0.29 ± 0.31
Marbled Murrelet	0.05 ± 0.05	0.13 ± 0.02	0.24 ± 0.05*	0.09 ± 0.05
Harlequin Duck	0.00	0.08 ± 0.11	0.02 ± 0.04	0.16 ± 0.13*
Rhinoceros Auklet	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.06 ± 0.02*

[a] Where each species reached its highest density is indicated by an asterisk.

(Angell and Balcomb 1982). Similarly, in Saanich Inlet, the highest densities of American Wigeon occurred near the mouths of streams, either in areas with extensive beaches or in shallow bays.

Barrow's Goldeneye were also most numerous off these long beach habitats, followed again by shallow bays. Whereas Vermeer (Part 5, this publication) found Barrow's Goldeneye to be most numerous along rocky shores, Angell and Balcomb (1982) claimed that this species preferred to feed off tidal flats, in estuaries, and in protected harbours.

Bonaparte's and California gulls also were most abundant along beach habitats. Both species were often encountered loafing in large numbers near the water. According to Manuwal *et al.* (1979), gravel or sand beaches are important roost sites for these species of gulls—a likely explanation for the high numbers observed.

Two bird species, Harlequin Duck (*Histrionicus histrionicus*) and Rhinoceros Auklet, were at their maximum densities along rocky shorelines. Numerous authors have reported that Harlequin Ducks prefer to forage in turbulent waters along rocky shores in search of crabs, amphipods, molluscs, and occasionally fish (Cottam 1939; Bent 1962; Dzinbal and Jarvis 1984). Rhinoceros Auklets feed primarily upon fish, hunting in estuaries and in entrance channels, especially over reefs (Angell and Balcomb 1982). The maximum number of Rhinoceros Auklets observed occurred in Finlayson Arm (Fig. 1) in late November, which coincided with the spawning of salmon in the Goldstream River at the head of the inlet.

6.3. Relationships between tidal position and the number of birds

Table 12 shows the results of the regression analyses between the proportion of birds (within each habitat type during each tidal height interval) and the midpoint of each interval. The populations of birds off beach habitats and along rocky shorelines showed no significant correlation with tide level. However, the numbers of birds in open waters and in shallow bays were strongly correlated with tidal fluctuations. As the water level rose, bays supported proportionately fewer birds, whereas open waters had more. The proportion of birds in bays (by tidal interval) was highly correlated (negatively, $P < 0.0025$) with the proportion of birds in open waters (Table 13). This suggested that, as the tide level increased, birds that had been feeding or roosting in shallow bays moved out into open waters. During falling tides, the reverse movement occurred. Morgan *et al.* (1987) found a significant ($P < 0.05$) decline in the proportion of birds feeding with increasing tidal height.

7. Recommendations for further studies

This study provides some indication of the species composition, seasonality, and habitat associations of

Table 12
Number of birds observed within each habitat type, by tidal interval[a]

Tide height (m above chart datum)	Open water	Shallow bay	Extensive beach	Rocky shore	Total present
1.00–1.25	79	4883	316	877	6 155
1.26–1.50	39	1187	202	310	1 738
1.51–1.75	60	593	216	342	1 211
1.76–2.00	682	4095	772	1322	6 871
2.01–2.25	94	1308	44	907	2 353
2.26–2.50	172	1339	751	905	3 167
2.51–2.75	5901	2519	715	754	9 889
2.76–3.00	2399	1361	1814	1222	6 796
3.01–3.25	4820	3005	1142	3456	12 423

[a] The proportion within each habitat type was regressed against the midpoint of each tidal interval. The results of the regression analysis are as follows: open water, $r = 0.8026$, $P < 0.005$; shallow bay, $r = -0.9420$, $P < 0.001$; extensive beach, $r = 0.3493$, ns; rocky shore, $r = 0.0896$, ns.

Table 13
Correlation matrix between the proportions of birds in each habitat type, by tidal interval

	Rocky shores	Extensive beaches	Shallow bays
Open waters	−0.4593	0.0301	−0.8231[a]
Shallow bays	0.0223	−0.429	–
Extensive beaches	0.0089	–	–

[a] $P < 0.0025$.

marine birds of Saanich Inlet. The study also indicates where further research is needed, as follows:
(1) Detailed studies on the preferred prey species should be initiated, including seasonal and daily variations in abundance and distribution and how the marine bird community responds to this.
(2) The relationships between tidal fluctuations, time of day, and the foraging behaviour of marine birds need to be studied.
(3) The importance of various natural and artificial habitat types to the diversity of marine birds requires further study.

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Part 6

History and conservation of birds

Archaeological evidence for use of the Strait of Georgia by marine birds

Keith A. Hobson and Jonathan C. Driver

1. Abstract

Archaeological evidence indicates that 49 marine and marine-associated bird species used 12 sites in the Strait of Georgia, which represent five habitat regions, in the period 3500 BC to 1800 AD. Thirty-five species were found in three sites at Boundary Bay and the lower Fraser River. Twenty-three species were identified from six sites on the Gulf Islands and the east coast of Vancouver Island. Three sites on southern Vancouver Island and Burrard Inlet yielded only 13 to 17 species. Archaeological evidence is generally consistent with the present use of the Strait of Georgia by marine birds. Exceptions include the following:
(1) more Black Scoter (*Melanitta nigra*) than Surf Scoter (*M. perspicillata*) bones were found at Boundary Bay;
(2) Brandt's Cormorant (*Phalacrocorax penicillatus*) bones were absent from sites near Active Pass; and
(3) Black-legged Kittiwakes (*Rissa tridactyla*) rather than Mew Gulls (*Larus canus*) were found in Gulf Island assemblages.

2. Résumé

Des documents archéologiques indiquent que 49 espèces d'oiseaux de mer ou associés à la mer ont été recensés à 12 endroits du détroit de Georgia représentant cinq régions sur le plan des habitats. On a reconnu la présence de 35 espèces à trois sites situés dans la baie Boundary et le bas-Fraser, 23 espèces à six sites des îles Gulf et de la côte est de l'île de Vancouver et 13 à 17 espèces seulement à trois sites situés dans le sud de l'île de Vancouver et l'inlet Burrard. En général, l'utilisation révélée par ces documents archéologiques correspond à l'utilisation actuelle du détroit par les oiseaux de mer. Quelques exceptions, toutefois, notamment :
(1) la présence de plus d'os de Macreuses à bec jaune (*Melanitta nigra*) que de Macreuses à front blanc (*M. perspicillata*) à la baie Boundary;
(2) l'absence d'os de Cormorans de Brandt (*Phalacrocorax penicillatus*) aux sites situés près du passage Active; et
(3) la présence de Mouettes tridactyles (*Rissa tridactyla*) au lieu de Goélands cendrés (*Larus canus*) dans les îles Gulf.

3. Introduction

Animal remains found in archaeological deposits provide a view of North American faunal distributions before the major impact of European settlement. In and around the Strait of Georgia, archaeological sites are found on the mainland, on Vancouver Island, and on most smaller islands. For about the last 5500 yr, human activity along the coast has resulted in the accumulation of dense shell middens (Fladmark 1986), and many of these sites include the remains of marine and marine-associated birds. In this paper, we summarize archaeological evidence for use of the Strait of Georgia by marine birds in the period 3500 BC to 1800 AD.

4. Problems with the archaeological record

Interpretation of avian remains from archaeological sites has a number of methodological problems. First, osteological differences between closely related bird species are often minor, so identification to the species level can be difficult. Furthermore, few good comparative collections of bird skeletons exist, so that zooarchaeologists may be forced to identify bones without complete information. Because of problems with identification to the species level, it is common practice simply to report higher taxa.

Once identifications have been made, the problem of interpretation remains. Many analysts note that wing bones are overrepresented archaeologically, probably because complete wings were used as decorative items (Ericson 1987). As well, wings may have been traded over long distances, resulting in the presence of bones that were not obtained locally. Human hunting presumably also concentrated on certain species, resulting in biased representation of different species. Vulnerability to hunting, palatability, and associated religious or mythical beliefs all influence the absolute and relative frequencies of occurrence of different species in archaeological sites.

There is currently some debate in paleontology about the utility of various measures of species abundance in paleoenvironmental reconstruction (Grayson 1981). Presence/absence data can mask important differences between species represented by single bones and others represented by hundreds of bones. However, unless one knows in some detail the mechanisms whereby the bones of a particular species were accumulated and preserved at a site, relative frequencies based on numbers of bones may also provide a misleading index of a species' local importance.

5. Methods

Many archaeological sites have been excavated around the Strait of Georgia, but few published studies exist, and fewer yet provide information on faunal remains. Archaeological sites are numbered using a national system. Information on the sites reported here is contained mainly in unpublished reports on file at the Heritage Conservation Branch, Victoria, BC.

This paper draws data from 12 sites (Table 1, Fig. 1) that broadly represent five habitat regions. These regions represent geographical or biological units (Wahl *et al.* 1981). Sites DkSg2, DiSc1, DhSb4, and DgRx5 are adjacent to the shallow broad banks of the central east coast of Vancouver Island; DfRu24 and DfRu8 are located in the sheltered waters of the Gulf Islands close to the nutrient-rich upwelling site of Active Pass; and DcRt1 and DcRu78, located near the southernmost entrance to the strait, are adjacent to more exposed waters. DhRr6 is located adjacent to the fjord-like habitat of Burrard Inlet and Indian Arm; the estuary and tidal mudflats of the Fraser River delta foreshore are represented by DgRr1, DgRr2, and DgRs1. DgRr2 is now located on the lower reaches of the Fraser River but would have been closer to the mouth of the river during part of its occupation. DgRr1 and DgRs1 are located on Boundary Bay. Data from these sites are presented in Table 2. Specimens that were not identified to species by the original analysts have not been included.

We considered marine species to include loons, grebes, cormorants, dabbling and diving ducks, gulls, and alcids. We also included data on marine-associated species, such as swans and geese, Great Blue Herons (*Ardea herodias*), Bald Eagles (*Haliaeetus leucocephalus*), and Northwestern Crows (*Corvus caurinus*). Shorebirds were not included, because they were rarely identified to species.

Data are reported by site. Although some of the sites span a period of about the last 5000 yr, there is no evidence for any change in species through time, and the presence/absence record refers to the entire period of a site's occupation. Where available, data on apparent species abundance have been cited under species accounts. However, many archaeological reports do not include quantitative information, and, even when such data are presented, the methods

Table 1
Locations and periods of occupation for archaeological sites in the Strait of Georgia

Site	Location	Approx. date	Reference
DkSg2	49°41'50"N 125°00'00"W	1000–1800 AD	Capes 1964
DiSc1	49°21'52"N 124°29'47"W	800–1300 AD	Bernick 1983
DhSb4	49°19'30"N 124°17'30"W	1500 BC - 400 AD	Lawhead 1980
DgRx5	49°09'15"N 123°53'10"W	2800 BC - 1200 AD	Murray 1982
DfRu24	48°51'50"N 123°20'50"W	1100 BC - 1300 AD	Haggarty and Sendey 1976
DfRu8	48°51'25"N 123°20'00"W	3500 BC - 1800 AD	Boucher 1976
DcRt1	48°26'02"N 123°18'10"W	400–1800 AD	Mitchell 1980
DcRu78	48°26'05"N 123°26'53"W	500–1800 AD	Mitchell 1981
DgRr1	49°03'10"N 122°52'50"W	700–1800 AD	Ham 1982
DgRs1	49°01'48"N 123°03'55"W	1500 BC - 400 AD	Lawhead 1980; Matson *et al.* 1980; Abbott, date unknown
DhRr6	49°18'48"N 122°55'22"W	300 BC - 1000 AD	Charlton 1970
DgRr2	49°09'30"N 122°56'25"W	2300 BC - 1000 AD	Calvert 1970; Boehm 1973

Figure 1
Locations of archaeological sites in the Strait of Georgia

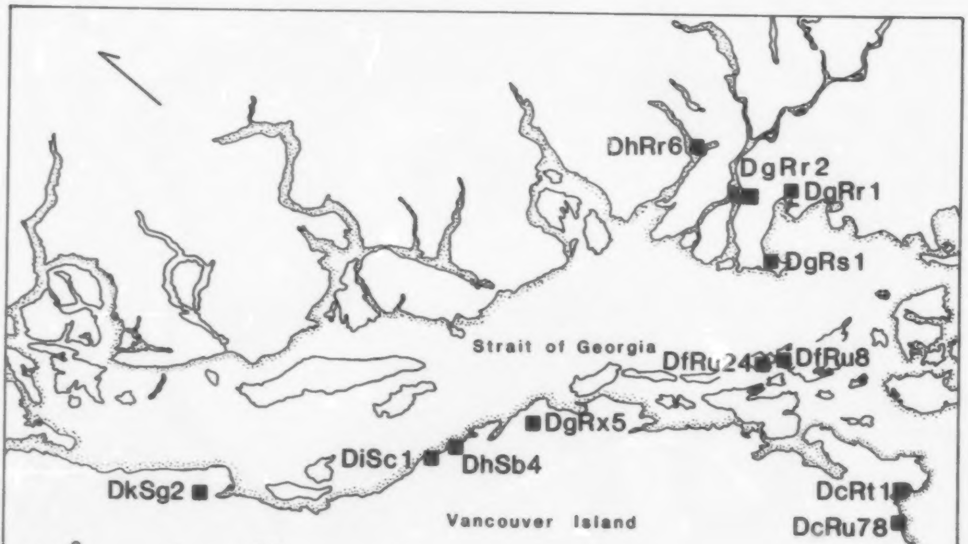

Table 2
Marine birds found in Strait of Georgia archaeological sites[a]

	A				B		C		D			E
Species	**DkSg2**	**DiSc1**	**DhSb4**	**DgRx5**	**DfRu24**	**DfRu8**	**DcRt1**	**DcRu78**	**DgRr1**	**DgRs1**	**DgRr2**	**DhRr6**
Gaviidae (loons)												
Gavia stellata			×							×	×	
G. pacifica						×				×		
G. immer					×	×		×			×	
Podicipedidae (grebes)												
Podilymbus podiceps							×					
Podiceps auritus										×		
P. grisegena		×	×							×	×	
P. nigricollis		×						×				
Aechmophorus occidentalis		×				×	×	×			×	
Phalacrocoracidae (cormorants)												
Phalacrocorax auritus			×			×		×		×	×	
P. penicillatus								×				
P. pelagicus				×		×						
Anatidae (swans, geese, ducks)												
Cygnus columbianus						×					×	
C. buccinator								×			×	
Anser albifrons						×			×		×	
Chen caerulescens										×		
Branta bernicla								×				
B. canadensis		×				×	×	×		×	×	×
Aix sponsa										×		
Anas crecca									×	×		
A. platyrhynchos	×					×			×	×	×	×
A. acuta						×			×	×		×
A. discors												×
A. clypeata												×
A. strepera		×				×						×
A. americana										×		×
Aythya collaris						×						
A. marila		×						×	×	×		
A. affinis	×											×
Histrionicus histrionicus												×
Clangula hyemalis						×		×	×	×		
Melanitta nigra										×		
M. perspicillata						×				×		×
M. fusca						×		×		×		
Bucephala clangula	×					×				×		
B. islandica									×			
B. albeola										×		×
Mergus merganser										×	×	
Laridae (gulls)												
Larus philadelphia						×			×		×	×
L. heermanni										×	×	
L. argentatus					×							
L. occidentalis					×						×	
L. glaucescens		×	×			×				×	×	
Rissa tridactyla						×						
Alcidae (alcids)												
Uria aalge			×			×	×	×			×	×
Cepphus columba			×									
Brachyramphus marmoratus								×			×	
Other												
Ardea herodias					×				×	×	×	
Haliaeetus leucocephalus	×	×		×	×				×	×	×	×
Corvus caurinus			×					×		×	×	

[a] A = east coast of Vancouver Island; B = Gulf Islands; C = south Vancouver Island; D = Boundary Bay/Fraser River; E = Burrard Inlet.

of quantification frequently differ from one site to another. For this reason, Table 2 simply records presence/absence of species.

6. Archaeological record

Forty-nine marine and marine-associated species were recorded in sites in the Strait of Georgia (Table 2). The nature of the data precludes detailed comparisons of relative species abundance or diversity between areas. However, sites at Boundary Bay produced the greatest number of species (n = 30), followed by those in the Gulf Islands (n = 23). These areas currently support large numbers of species at least seasonally. Species compositions were compared between sites using Sorenson quotients of similarity (Southwood 1966; Table 3). Here a value of "0" indicates no species overlap, whereas a value of "1" indicates that both sites have identical species composition. Similar values were found for most comparisons, with the exception of Burrard Inlet and south Vancouver Island regions, which showed little similarity. Below we consider species groups separately.

Table 3
Quotients of species similarity between regions[a]

	A	B	C	D	E
A	1.0				
B	0.44	1.0			
C	0.46	0.38	1.0		
D	0.32	0.48	0.28	1.0	
E	0.37	0.42	0.15	0.36	1.0

[a] Conventions as in Table 2.

6.1. Loons

Three species of loons were recorded from all areas except Burrard Inlet. Where present, the Red-throated Loon (*Gavia stellata*) was represented only by single bones. Pacific Loons (*G. pacifica*) appeared abundant at DfRu8, where 93 bones were excavated. This is consistent with the present distribution of this species, which is seasonally abundant in Active Pass (Vermeer 1983). Similarly, Common Loons (*G. immer*) appeared to be most abundant at this site, where 37 bones were found, compared with only a single bone at DcRu78.

6.2. Grebes

Grebes were represented by five species in all areas except Burrard Inlet. This conforms broadly to present patterns of fall and winter use of the Strait of Georgia. Horned Grebes (*Podiceps auritus*) were found only at one site, despite their present wintering abundance throughout the region. Western Grebes (*Aechmophorus occidentalis*) appeared to be abundant at the Gulf Islands and south Vancouver Island sites, where 64 and 22 bones were found, respectively. This is consistent with present seasonal patterns of distribution in the Gulf Islands (Vermeer 1983) and off southern Vancouver Island.

6.3. Cormorants

All three cormorant species known to occur in the Strait of Georgia were represented in the archaeological record. Double-crested Cormorants (*Phalacrocorax auritus*) were present in sites from each area except Burrard Inlet. They appeared to be most numerous in the Gulf Islands region, where 31 bones (DfRu8) were identified. Drent and Guiguet (1961) suggested that this species colonized the inner coast of British Columbia and Washington starting in the early 1920s. They speculated further that climatic amelioration, possible increases in food supply, and the cessation of egg collecting could have caused the increases (see also Vermeer and Rankin 1984). Archaeological evidence suggests that such increases may actually represent a recolonization of this area. Pelagic Cormorants (*P. pelagicus*) have similarly increased throughout the Strait of Georgia (Drent and Guiguet 1961; Vermeer and Rankin 1984), but their presence in the archaeological record again suggests that such increases do not necessarily indicate recent colonization. Unfortunately, without information on seasonality or the presence of nestling bones, it is impossible to determine whether cormorants from sites in the Strait of Georgia represent breeding individuals.

Brandt's Cormorants (*P. penicillatus*) occurred only at DcRu78 off the south coast of Vancouver Island. This was unexpected, because this species currently occurs in large numbers in Active Pass from November to April (Vermeer 1977). This absence cannot be explained in terms of human seasonality in site use, because excavations here show comparatively large numbers of Pacific Loons and Western Grebes, both of which occur primarily in the fall. At present, Brandt's Cormorants move into the strait, and particularly into Active Pass, after breeding at sites as far south as the Farallon Islands, California (Vermeer 1977). It is possible that this movement occurred recently. This species expanded its breeding range into British Columbia only since 1965 (Stirling and Buffam 1966; Vermeer *et al.* 1976), and only a few hundred are known to nest in British Columbia, Alaska, Washington, and Oregon (Vermeer *et al.* 1976).

6.4. Swans and geese

Swans were found at only three excavations and may have been restricted to a few wintering or migratory stopover sites. Tundra Swans (*Cygnus columbianus*) were present at the Gulf Islands site of DfRu8 and the Fraser River estuary site of DgRr2. A single Trumpeter Swan (*C. buccinator*) was identified at DcRu78 on the south coast of Vancouver Island, and this species was present at DgRr2. Greater White-fronted Geese (*Anser albifrons*) were found in the Gulf Islands (DfRu8) and the Fraser River estuary (DgRr1, DgRr2). This suggests a more extensive migratory or wintering use of the Strait of Georgia than exists today (see also Timm and Dau 1979). This species is currently classed as rare or casual on the Fraser River estuary (Vancouver Natural History Society checklist). Snow Geese (*Chen caerulescens*) were found only at the Boundary Bay site of DgRs1, which is consistent with this species' present wintering use of the Fraser River estuary. Canada Geese (*Branta canadensis*) appeared to be the most widespread of all these species—it occurred in sites representing all areas of the strait. The occurrence of Brant (*B. bernicla*) bones at DgRs1 and DcRu78 is consistent with this species' present pattern of migration and stopover on the east and west coasts of the Strait of Georgia.

6.5. Dabbling ducks

Dabbling ducks were uncommon in sites along the east and south coasts of Vancouver Island. Boundary Bay sites produced the most species, with only Northern Shoveler (*Anas clypeata*) and Gadwall (*A. strepera*) being noticeably absent. Green-winged Teal (*A. crecca*) and Blue-winged Teal (*A. discors*) were found only at sites in this area. Five species, including the only occurrence of the Northern Shoveler, were found at the Burrard Inlet site. Historically, suitable waterfowl habitat was provided by extensive tidal mudflats and marshes, particularly along the north shore and eastern region of the inlet. Mallard (*A. platyrhynchos*), Northern Pintail (*A. acuta*), and Gadwall were found in the Gulf Islands site of DfRu8. Noticeably absent from the Gulf Islands assemblage was the American Wigeon (*A. americana*), which currently concentrates around estuarine shores there in autumn (Vermeer 1983). A variety of ducks was found at DgRr2 but not identified to species (Boehm 1973).

6.6. Diving ducks

Diving ducks were found in all areas, but greatest species diversity occurred in assemblages from Boundary Bay. Black Scoter (*Melanitta nigra*) and Barrow's Goldeneye (*Bucephala clangula*) occurred only in these sites. At present, Black Scoters are the least common scoter in Boundary Bay and elsewhere in south-coastal British Columbia (Vermeer and Levings 1977; Vermeer and Bourne 1984). This contrasts with vast numbers of Surf Scoters (*M. perspicillata*) and several hundred White-winged

Scoters (*M. fusca*) that use the bay, particularly in August (Vermeer and Levings 1977). However, 25 bones of Black Scoter were found at DgRs1 compared with 15 and 16 bones for Surf and White-winged scoters, respectively. The occurrence of 32 bones identified as Ring-necked Duck (*Aythya collaris*) in the Gulf Islands assemblage of DfRu8 is noteworthy, although this species is classed as being common in winter within the Victoria Natural History Society checklist area.

Despite the tens of thousands of diving ducks that currently occur in autumn and spring over the banks of eastern Vancouver Island (Vermeer 1983), archaeological sites in this area recorded only Greater (*Aythya marila*) and Lesser (*A. affinis*) scaup and Common Goldeneye. Oldsquaw (*Clangula hyemalis*), Surf Scoters, and White-winged Scoters occurred in the Gulf Islands site of DfRu8. These species are the most common diving ducks in this area at present (Vermeer 1983).

6.7. Gulls

Six species of gulls were found at archaeological sites representing all areas except the south coast of Vancouver Island. The Gulf Islands sites recorded the greatest species diversity, followed by DgRr2 on the Fraser River estuary. At DfRu8, 37 bones identified as Bonaparte's Gull (*Larus philadelphia*) were found, as well as 124 bones of Glaucous-winged Gulls (*L. glaucescens*). Both these species are seasonally numerous in Active Pass (Vermeer *et al.* 1987). Notably absent from this assemblage were bones of Mew Gulls (*L. canus*). This species is currently numerous in Active Pass from February to March (Vermeer *et al.* 1987). Also of note at DfRu8 was the presence of 21 bones identified as Black-legged Kittiwake (*Rissa tridactyla*). This species is currently classed as an uncommon migrant in this area (Victoria Natural History Society checklist). The Gulf Islands site of DhSb4 recorded the only occurrence of Herring Gull (*L. argentatus*). Sites along the east coast of Vancouver Island recorded only Glaucous-winged Gulls, and Heerman's Gull (*L. heermani*) was present at DgRr2 and was represented by a single bone at the Boundary Bay site of DgRs1.

6.8. Alcids

Common Murres (*Uria aalge*) were found in sites representing all areas except Boundary Bay. This species appeared to be numerous in the Gulf Islands assemblage (DfRu8), where 128 bones were identified. Only a single bone was identified at DhSb4 on the east coast of Vancouver Island. A single bone of a Pigeon Guillemot (*Cepphus columba*) was found at DhSb4 on the east coast of Vancouver Island. Marbled Murrelet (*Brachyramphus marmoratus*) remains occurred only at DcRu78 on the south coast of Vancouver Island and at DgRr2 on the lower Fraser River, where a single bone was identified.

6.9. Other species

Great Blue Herons were found at DfRu24 on the Gulf Islands and at all sites on the Fraser River estuary. These areas currently support significant heron rookeries (R. Butler, pers. commun.). Bald Eagles were found in sites from all areas except those on southern Vancouver Island and were likely taken for cultural purposes (Barnett 1939, 1955). Northwestern Crows occurred in sites from all areas except those in the Gulf Islands and Burrard Inlet.

7. Recommendations for further studies

In general, archaeological evidence for use of the Strait of Georgia by marine birds suggests that little has changed during the last 5500 yr. However, few of the sites in this analysis pertain to the earlier part of this time period. Larger, better-dated samples from all periods are required before strong conclusions can be made about historical changes in species composition. Some species require further investigation. The species identification of cormorant bones from DfRu8 should be confirmed. Further investigations at this and other sites might reveal historical patterns of colonization and postbreeding dispersal, particularly by Double-crested and Brandt's cormorants. Identifications of Black-legged Kittiwake bones found at DfRu8 should also be confirmed. Finally, in order that valuable information based on avian archaeological remains is not lost and is used effectively, stronger liaison between the archaeological and ornithological communities is required.

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Mariculture and bird interactions in the Strait of Georgia

Kees Vermeer and Ken H. Morgan

1. Abstract

The development of the mariculture industry in the Strait of Georgia, which consists primarily of finfish and shellfish, is discussed. Most finfish farms are involved in raising salmon, and most of the shellfish farms grow oysters. There were at least 83 licensed finfish and 243 licensed shellfish farms in the Strait of Georgia in May 1988.

The direct impacts of mariculture on marine birds are the accidental drowning in net pens and the shooting of birds by farm operators. Indirect effects are the alteration of the birds' habitat and food and the contamination of this food. The needs of mariculture may also compete with those of marine birds for euphausiids, an important prey for planktivorous birds.

2. Résumé

La mariculture est en progression dans le détroit de Georgia. L'industrie se divise en deux grands segments : les piscicultures, qui produisent presque toutes des saumons, et le secteur des mollusques et crustacés, constitué presque entièrement d'élevages d'huîtres. En mai 1988, on comptait dans le détroit au moins 83 établissements approuvés dans le secteur des poissons et 243 dans celui des mollusques et crustacés.

La mariculture a des répercussions directes sur les oiseaux de mer : ceux-ci se prennent parfois dans les filets des cages et sont abattus par les mariculteurs. Elle a aussi des répercussions indirectes en modifiant l'habitat et la nourriture des oiseaux et en causant la contamination de leurs sources de nourriture. Il peut également y avoir un conflit entre les besoins de la mariculture et ceux des oiseaux de mer en ce qui a trait aux Euphausiacés qui constituent une source importante de nourriture pour les oiseaux planctivores.

3. Introduction

There are many threats to marine birds in the Strait of Georgia—e.g., physical destruction of habitat, oil spills, contamination by organochlorine pesticides and heavy metals, and human disturbance and predation. The present, rapidly expanding mariculture industry in the Strait of Georgia is recognized as a potential new threat to marine birds. The objectives of this paper are to provide a brief overview of mariculture development in the Strait of Georgia and to discuss the threat the industry poses to marine birds.

4. Mariculture industry

4.1. Finfish tenures

Most marine finfish tenures in British Columbia involve salmon. The salmon are raised in open, rectangular net pens of varying size. A salmon farm is generally composed of many of these pens moored together. The total surface area of the 83 salmon farm operations in the Strait of Georgia in May 1988 was estimated to be 417 ha. The average surface area of a salmon farm was calculated to be 5.1 ± 3.4 (SD) ha, and individual areas ranged from 0.6 to 19.2 ha. The salmon are fed pellets by hand and/or by automatic feeder. Bourne and Brett (1984) estimated that it takes 2-3 yr from farm start-up until the salmon can be marketed.

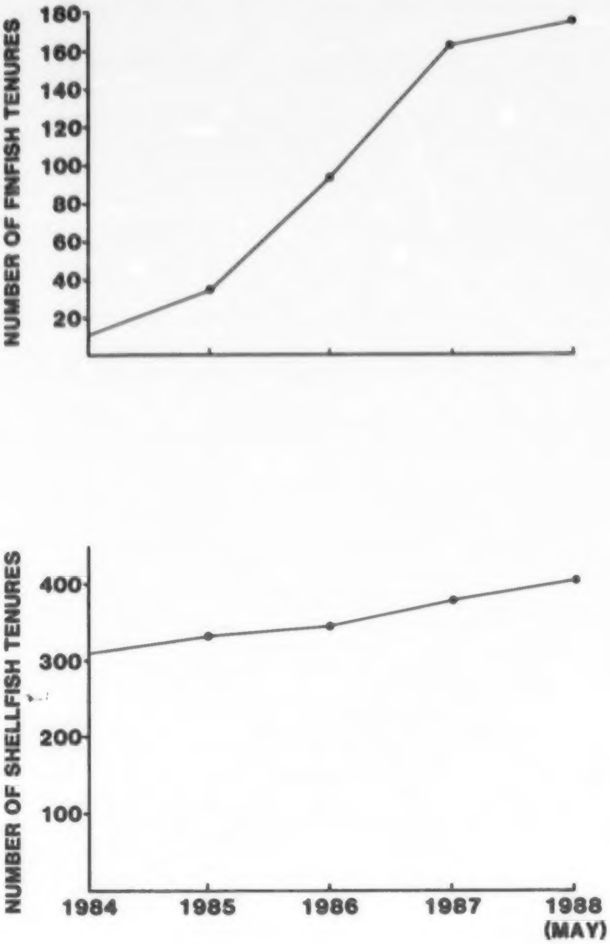
Salmon mariculture in British Columbia has grown from 10 licensed farms in 1984 to 180 in May 1988 and continues to increase (Fig. 1). The 83 farms located in the Strait of Georgia are mainly found in sheltered inlets around Quadra and Nelson islands, at the entrance to Jervis Inlet, and in Sechelt Inlet (Fig. 2).

4.2. Shellfish tenures

Most shellfish farms in British Columbia are involved with oysters. The Pacific oyster (*Crassostrea gigas*), first introduced to British Columbia in 1912 (1913), is the most commonly farmed species. Oysters are induced to spawn in a hatchery. The larvae are grown in tanks until they reach 1-5 cm in size; they are then introduced to firm gravel, sand, or mud, or are suspended in the water column. Oysters are harvested when 3 yr old or older. Of the 243 shellfish tenures in the Strait of Georgia in May 1988, 239 were for oysters, three for mussels, and one for clams. The average surface area of oyster tenures was 4.2 ± 6.2 (SD) ha (range 0.14–50 ha). The overall surface area of these 243 tenures was estimated to be 1018 ha in May 1988.

In British Columbia, the shellfish industry has existed much longer than that for finfish. There were at least 300 farms in existence in British Columbia in 1984, and their number continues to grow, although at a much lower rate than that for finfish (Fig. 1). Of the 402 shellfish tenures in British Columbia in May 1988, 60% were located in the Strait of Georgia. The aggregations of shellfish tenures were in the same regions as those for finfish, as well as around Denman, Hornby, Lasqueti, and the Gulf islands

Figure 1
Growth of finfish and shellfish operations in British Columbia



(Fig. 3). Oyster tenures extended farther across the northern sector of the strait than did those of salmon (cf. Figs. 2 and 3).

4.3. Algae tenures

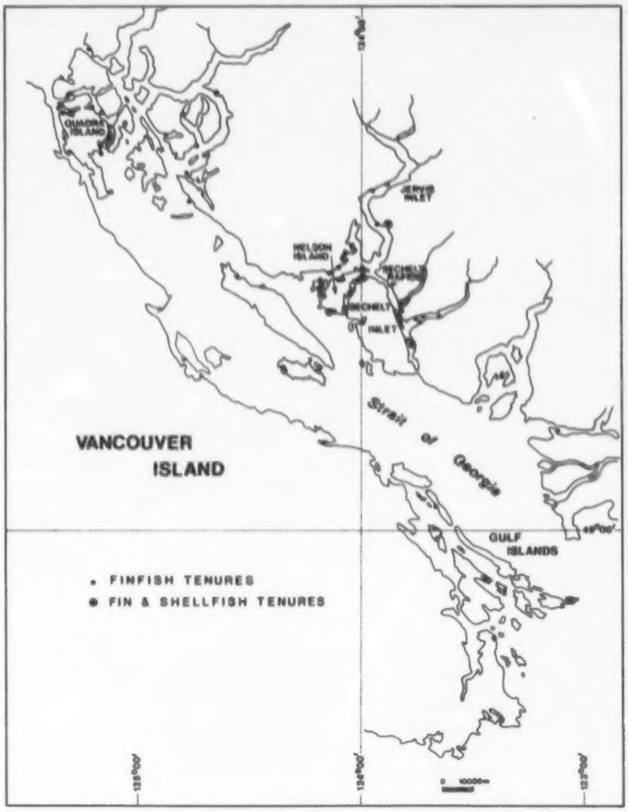
In May 1988, there were also five licensed algae tenures in British Columbia. Of the algae, *Porphyra* is used to produce "nori" for sushi bars, whereas *Laminaria groenlandica* and *L. sacarina* are grown to produce "kombu" for the Japanese market.

5. Mariculture–bird interactions

5.1. Effects on mariculture

The main impacts of marine birds on mariculture production appear to be predation and net fouling (Booth and Rueggeberg 1988). Booth and Rueggeberg (1988) canvassed fish farmers through both correspondence and personal contact in British Columbia and found that Great Blue Herons (*Ardea herodias*) were cited as most frequently preying on salmon fry, whereas ducks, grebes, loons, and cormorants attempted to prey on penned stock. These authors reported that predation by birds was not a major problem at oyster farms. Mussel farms, on the other hand, suffer greatly from predation by Surf Scoters (*Melanitta perspicillata*) and Barrow's Goldeneyes (*Bucephala islandica*) (Vermeer 1981; Bourne and Brett 1984).

Figure 2
Distribution of finfish tenures in the Strait of Georgia, May 1988



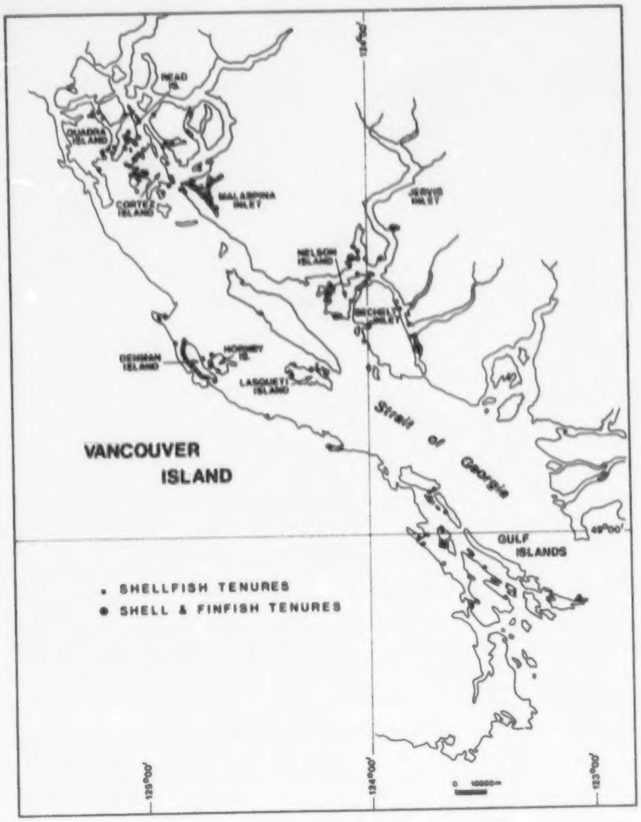
5.2. Direct effects on birds

Booth and Rueggeberg (1988) also reported that birds are directly affected by mariculture by becoming entangled in submerged nets (diving birds) and in predator nets (herons) and consequently being drowned, and by being shot or poisoned. One person informed the first author that he observed a fish farmer shooting an Osprey (*Pandion haliaetus*) in the vicinity of his farm.

5.3. Indirect effects on birds

Fish farming can affect birds indirectly through alteration or contamination of their habitat and food supply. The decomposition of excess food and the excretion by many confined fish lead to eutrophication, algal blooms, and oxygen depletion in waters at or near farms; sewage fungus may cover the bottom beneath net pens in poorly flushed waters (Leonardsson and Näslund 1983; Rosenthal 1985). The benthic invertebrate community has been observed to be greatly altered near fish farming operations (Ackefors and Södergren 1985); these changes may result in decreased prey availability. Antifoulants, which consist of a wide range of fungicides and pesticides, as well as antibiotics used to prevent disease, may contaminate the food of marine birds when used on net pens. One such antifoulant, tributyltin (TBT), now prohibited in Canada, caused mortality of juvenile salmon, acute toxicity in bivalve larvae, and chronic ill effects in adult oysters and crustaceans (Halsey 1988). Since the banning of TBT,

Figure 3
Distribution of shellfish tenures in the Strait of Georgia, May 1988



the mariculture industry has considered the large-scale application of NUVAN, which contains dichlorovos (Duff 1988). Dichlorovos is reported to be selectively toxic to the central nervous system of arthropods.

Besides affecting the food supply through contamination or habitat alteration, fish farmers may directly compete with marine birds for food. An example is the harvesting of euphausiids. The euphausiid fishery in British Columbia is small at present (500 t, mostly harvested in Jervis Inlet) but is projected to increase to 100 000 t by 1995 if euphausiids are used as the sole protein source in salmon feeds (J. Fulton, pers. commun.). One important locality where euphausiids are harvested at present is the tidally active area at Sechelt Rapids (Fig. 2) (B. McLelland, pers. commun.). Thousands of Bonaparte's (*Larus philadelphia*) and Mew (*L. canus*) gulls feed on euphausiids at this location during spring (KV, pers. obs.). In the Strait of Georgia, there are relatively few tidally active areas where euphausiids are accessible in large quantities to surface-feeding planktivorous birds during daylight. If the trend of harvesting euphausiids in such areas continues, many planktivorous birds may be detrimentally affected by the loss of a high-energy food usually obtained prior to breeding (Vermeer *et al.* 1987).

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Toxic chemicals in Great Blue Heron (*Ardea herodias*) eggs in the Strait of Georgia

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1. Abstract

Various toxic substances are continuously deposited in the Strait of Georgia in urban sewage and runoff, industrial wastes, agricultural runoff, mine leachates, ocean dumping of industrial wastes, fugitive discharges from ships, and accidental spills. The damage these substances cause when they enter the environment has been a concern for several decades. Analysis of Great Blue Heron (*Ardea herodias*) eggs collected over the past 10 yr shows that levels of several toxic chlorinated hydrocarbons—polychlorinated biphenyls (PCBs), dichlorodiphenyldichloroethylene (DDE), dieldrin, and heptachlor epoxide—have fallen in estuarine and coastal areas of the southern Strait of Georgia. Today the burden of those chemicals in herons nesting near urban and industrial areas is no greater than that of herons nesting in comparatively pristine areas. High levels of dioxins and furans were discovered recently in the eggs of Great Blue Herons nesting near wood processing operations on the strait. Dioxins are potent avian embryotoxins and may be implicated in the failure of a heron colony located near a pulp mill to fledge young in 1987. These studies clearly demonstrate that the Great Blue Heron is a valuable indicator of the condition of estuarine and coastal environments in the Strait of Georgia.

2. Résumé

Le détroit de Georgia reçoit de façon continue diverses substances toxiques à cause des eaux usées et eaux de ruissellement des villes, des déchets industriels, des eaux de ruissellement des terres agricoles, des eaux de mine, de l'immersion de déchets industriels en mer, des fuites des navires et des déversements accidentels. On se préoccupe depuis plusieurs décennies des dommages que ces substances causent à l'environnement. L'analyse des oeufs de Grands hérons (*Ardea herodias*) cueillis au cours des 10 dernières années indique une diminution des concentrations de plusieurs hydrocarbures chlorés toxiques — biphényles polychlorés (BPC), dichlorodiphényldichloroéthylène (DDE), dieldrine et époxyde d'heptachlore — dans les zones estuariennes et côtières du sud du détroit. À l'heure actuelle, la charge de ces composés chimiques chez les hérons nichant près des zones urbaines et industrielles n'est pas plus élevée que chez les hérons nichant dans des zones comparativement non polluées. Des dioxinnes et des furannes en concentrations élevées ont été découverts récemment dans des oeufs de Grands hérons nichant près d'établissements de traitement du bois de la région. Les dioxinnes, qui sont des produits très toxiques pour les embryons d'oiseaux, pourraient être en cause dans l'échec d'envol observé en 1987 dans une colonie d'hérons située près d'une usine de pâte. Les études démontrent clairement que le Grand héron constitue un indicateur utile de l'état des milieux estuariens et côtiers du détroit de Georgia.

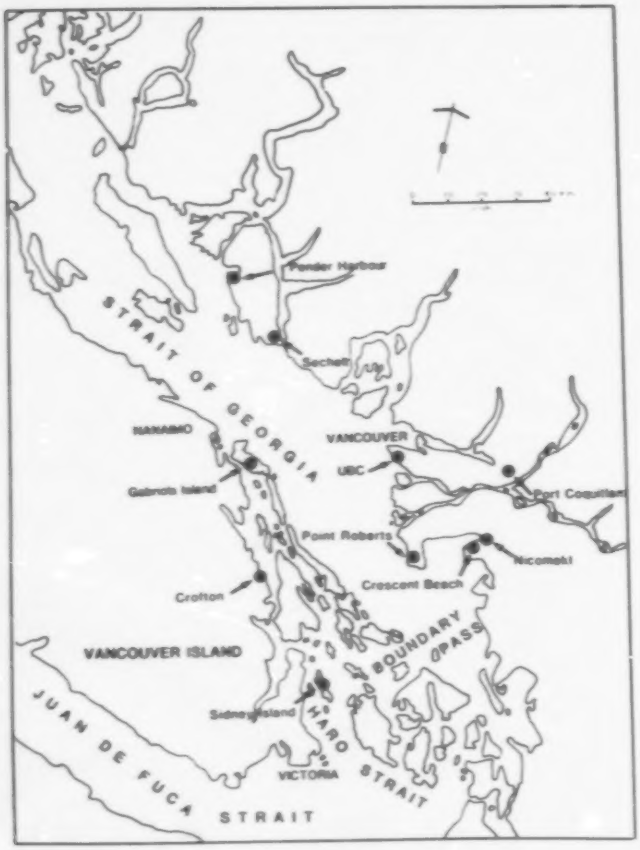
3. Introduction

Waldichuk (1983) reviewed pollution in the Strait of Georgia and noted that the physical behaviour of marine systems determines in large measure how polluted they become with a given amount of waste input. The size of the system and the rate that water is exchanged with unpolluted water are critical factors in the model. The Strait of Georgia is a large system having a relatively unrestricted connection with the open sea through Boundary Pass, Haro Strait, and Juan de Fuca Strait (Fig. 1) (Waldichuk 1957). The replacement rate for its deep waters is estimated to be once per year. The large size of the system and relatively rapid replacement rate likely account for the comparatively low pollution levels found in offshore water. The physical behaviour of the system also influences where wastes are deposited. For example, Waldichuk (1983) noted that a mixing zone at the southern entrance to the strait could take surface contaminants into the water column in the Boundary Pass area and deposit them in the deep zone. Factors such as tides, winds, river runoff, coriolis, and centrifugal forces also determine circulation patterns of water in the strait and, in considerable measure, where contaminants are deposited.

The impact of urban and industrial wastes discharged to the Strait of Georgia on resident and overwintering water birds has received scant attention—likely because there has been no visible reason for concern. Little evidence has been found that deteriorating water quality, or the presence of toxic chemicals, is significantly impacting bird populations in the strait. Vermeer and Peakall (1979) were concerned that high levels of metals in wastewater were accumulating in Surf Scoters (*Melanitta perspicillata*) and Greater Scaup (*Aythya marila*) in the Fraser River delta intertidal area. Although significant differences in concentration of some metals between the species and among different sites on the estuary were found, levels in all cases were within the normal range.

McKelvey *et al.* (1980) reported that a significant number of wintering water birds were killed in Vancouver Harbour when vegetable oil was accidentally spilled while

Figure 1
Location of Great Blue Heron colonies on the Strait of Georgia



being loaded onto a ship. It was noted that relatively small spills of nonpetroleum oil can be more hazardous to birds than much larger spills of petroleum. Between 1974 and 1978, 176 petroleum spills oiled 50 birds, and three vegetable oil spills affected more than 500 birds.

Although pollution has caused little noticeable harm to birds using the Strait of Georgia, the importance of monitoring the quality of the environment and of being conscious of the potential impact on water birds if it deteriorates significantly has not been completely ignored. In 1977, the Canadian Wildlife Service implemented a program to survey and monitor organochlorine levels in Great Blue Herons nesting around the Strait of Georgia. The program had three goals:
(1) to determine organochlorine levels in a species at the top of the estuarine food chain as an indicator of environmental quality;
(2) to track changes in pollution levels over time; and
(3) to determine if the health of the birds is affected by toxic substances in the environment.
This paper describes some of the results of that program.

4. Methods

Between 1977 and 1979, eggs were collected from Great Blue Heron nests in colonies on the Endowment Lands of the University of British Columbia (UBC) and at Port Coquitlam, Point Roberts in Washington State, Crescent Beach, Pender Harbour, and Sechelt. Based on the results of those analyses, a program was undertaken to monitor the most contaminated colony—UBC—on a 5-yr basis, and further samples were collected there in 1982 and 1987. Three additional colonies at Crofton, Nicomekl (believed to be the herons from the colony at Crescent Beach, which was abandoned in 1981), and Sidney Island were sampled in 1986 and 1987. Figure 1 shows the location of the colonies sampled.

Nest trees were climbed, and a single egg was removed from each of 10 or more nests in each colony. As soon as possible following collection, the contents of the eggs were transferred to acetone-rinsed jars with foil-lined caps and frozen at −25°C until analyzed. Samples collected in 1977–82 were analyzed by the Ontario Research Foundation following procedures described by Reynolds and Cooper (1975). The samples collected in 1987 were analyzed at the National Wildlife Research Centre using methods described by Peakall *et al.* (1986). Polychlorinated biphenyl (PCB) levels were expressed as a mixture of 1:1 Aroclor 1254:1260 so that comparisons could be made with earlier data. With recent methodology, the sum of congeners can be calculated, providing a more accurate measure of PCB level. The sum of congeners can be approximated by dividing the 1:1 Aroclor 1254:1260 values presented in the tables by 2.27. All residue data are expressed on a wet-weight basis for the reasons discussed by Peakall and Gilman (1979). The residue data are not normally distributed; consequently, medians have been used as measures of central tendency, and nonparametric analysis of variance (Kruskall-Wallis) has been used to test for differences between samples. A significance level of $P < 0.05$ was applied to all statistical tests.

5. Results

Residues of PCBs, dichlorodiphenyldichloroethylene (DDE), dieldrin, heptachlor epoxide, oxychlordane, and hexachlorobenzene (HCB) were detected in nearly all the eggs collected in 1977–79 (Table 1). The highest median levels of DDE, dieldrin, heptachlor epoxide, and PCB were found in eggs from the colony on the UBC Endowment Lands. Median levels of those contaminants were significantly higher in eggs from the UBC colony than in eggs from Sechelt and Pender Harbour. Median levels of dieldrin and PCB in eggs from the UBC colony were also significantly higher than levels in eggs from Point Roberts and Crescent Beach. Eggs from the Port Coquitlam colony contained significantly higher median levels of DDE and heptachlor epoxide than did eggs from Sechelt, and Pender Harbour and Sechelt, respectively. Levels of most of the contaminants in eggs from Point Roberts and Crescent Beach were generally intermediate.

Eggs from the Pender Harbour, Sechelt, and Crescent Beach colonies all contained significantly higher median levels of oxychlordane than did eggs from Port Coquitlam. Levels in eggs from the Pender Harbour colony were also significantly higher than those from UBC. Median HCB levels were significantly higher in eggs from Sechelt than in eggs from all the other colonies.

Most organochlorine residues in Great Blue Heron eggs collected from the UBC colony over a 10-yr period declined significantly (Table 2). Median levels of most contaminants were generally higher in 1977 and 1982 than in 1987. For example, significantly higher median levels of DDE, dieldrin, and PCB were found in 1977 and 1982 than in 1987. In the case of heptachlor epoxide, only the median level in 1977 was significantly higher than that in

Table 1
Organochlorine residue levels in Great Blue Heron eggs from six colonies, 1977–79

		Residue levels (mg·kg^{-1} wet weight), median (range in parentheses)					
Colony	*n*	DDE	Dieldrin	Heptachlor epoxide	Oxychlordane	HCB	PCB
UBC Endowment Lands	12	2.01 (0.83–5.84)	0.065 (0.030–0.340)	0.065 (0.030–0.130)	0.010 (0.009–0.020)	0.020 (0.010–0.050)	17.50 (6.92–50.20)
Port Coquitlam	12	2.00 (0.23–3.09)	0.035 (0.009–0.210)	0.035 (0.000–0.500)	0.000 (0.000–0.040)	0.025 (0.010–0.280)	6.47 (0.65–77.5)
Point Roberts	12	1.08 (0.22–10.80)	0.020 (0.010–6.010)	0.020 (0.010–0.310)	0.015 (0.009–0.240)	0.020 (0.010–0.060)	3.54 (1.21–20.9)
Crescent Beach	10	0.89 (0.71–1.24)	0.030 (0.009–0.060)	0.020 (0.009–0.080)	0.025 (0.009–0.050)	0.020 (0.020–0.050)	3.60 (2.28–5.65)
Pender Harbour	12	0.90 (0.14–2.59)	0.020 (0.010–0.050)	0.010 (0.009–0.020)	0.030 (0.010–0.040)	0.030 (0.010–0.050)	4.65 (0.84–33.2)
Sechelt	12	0.39 (0.03–2.10)	0.020 (0.009–0.440)	0.009 (0.000–0.030)	0.020 (0.010–0.120)	0.050 (0.030–0.070)	3.06 (1.96–9.71)

Table 2
Organochlorine residue levels in Great Blue Heron eggs from a colony in the Endowment Lands of the University of British Columbia, 1977–87

		Residue levels (mg·kg^{-1} wet weight), median (range in parentheses)					
Year	*n*	DDE	Dieldrin	Heptachlor epoxide	Oxychlordane	HCB	PCB
1977	12	2.01 (0.83–5.84)	0.065 (0.030–0.340)	0.065 (0.030–0.130)	0.010 (0.009–0.020)	0.020 (0.010–0.050)	17.50 (6.92–50.2)
1982	11	1.28 (0.28–2.83)	0.040 (0.020–0.860)	0.020 (0.010–0.710)	0.040 (0.020–0.180)	–	9.50 (3.64–30.2)
1987	27	0.419 (0.12–7.22)	0.014 (0.007–1.64)	0.012 (0.004–0.371)	0.021 (0.007–0.185)	0.015 (0.007–4.55)	2.89 (0.506–9.4)

Table 3
Organochlorine residue levels in Great Blue Heron eggs from four colonies, 1986–87

		Residue levels (mg·kg^{-1} wet weight), median (range in parentheses)					
Colony	*n*	DDE	Dieldrin	Heptachlor epoxide	Oxychlordane	HCB	PCB
UBC Endowment Lands	27	0.419 (0.12–7.22)	0.014 (0.007–1.64)	0.012 (0.004–0.371)	0.021 (0.007–0.185)	0.015 (0.007–4.55)	2.89 (0.506–9.4)
Crofton	10	0.112 (0.043–0.286)	0.008 (0.006–0.021)	0.005 (0.003–0.011)	0.012 (0.005–0.021)	0.013 (0.001–0.029)	1.45 (0.54–3.71)
Nicomekl	5	0.41 (0.27–1.67)	0.016 (0.007–0.080)	0.017 (0.008–0.027)	0.017 (0.016–0.048)	0.009 (0.007–0.017)	1.95 (1.32–3.38)
Sidney Island	4	0.09 (0.05–0.16)	0.005 (0.002–0.008)	0.004 (0.001–0.006)	0.007 (0.003–0.019)	0.008 (0.006–0.14)	1.05 (0.35–3.54)

1987. The median level of oxychlordane was significantly higher in 1982 than in both 1977 and 1987, whereas there was no significant difference in HCB level between years.

Median PCB levels in eggs fell significantly from 17.5 mg·kg^{-1} in 1977 to 2.89 mg·kg^{-1} in 1987; median DDE levels also fell significantly from 2.01 to 0.419 mg·kg^{-1}.

A survey of organochlorine residues in eggs from four colonies in 1986 and 1987 (Table 3) showed no significant differences among the colonies in median levels of DDE, dieldrin, HCB, and PCB. Eggs from Crescent Beach had significantly higher median levels of heptachlor epoxide and oxychlordane than did eggs from Sidney Island and Crofton, respectively.

6. Discussion

Over the years, various criteria have been proposed by which to assess the suitability of birds as indicators of environmental pollution. These were recently discussed and elaborated on by Gilbertson *et al.* (1987) as they pertain to seabirds as indicators of marine pollution. Judged on those criteria, the Great Blue Heron is an excellent indicator of estuarine habitats in the Strait of Georgia. Herons are abundant in the area, and colonies are distributed throughout the strait (Mark 1976; Forbes *et al.* 1985*a*). Their prey have been described by Paine (1972), Krebs (1974), and Simpson (1984). Reproductive success in

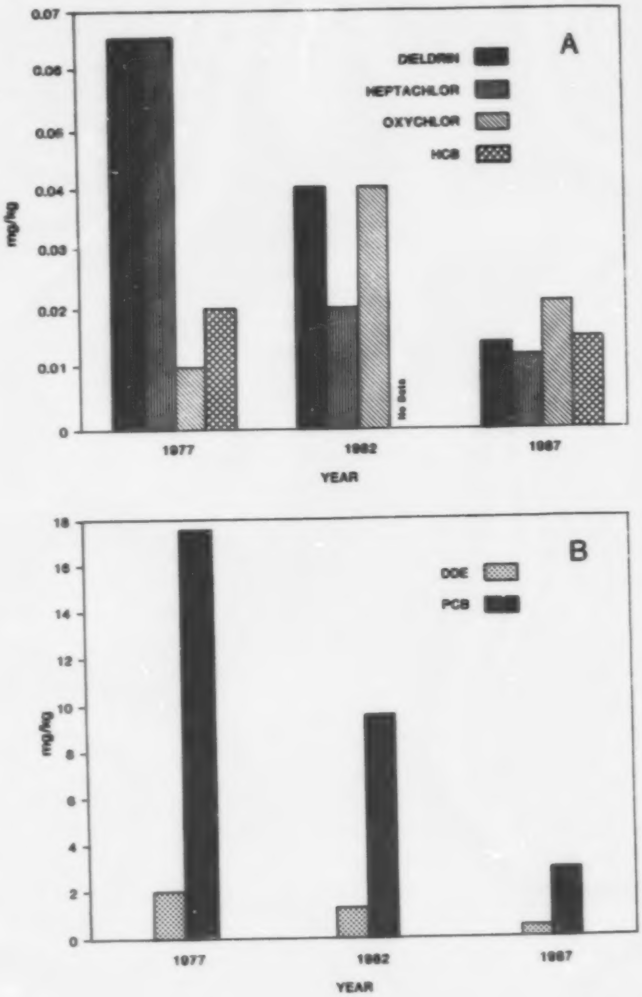
British Columbia was analyzed by Forbes *et al.* (1985*b*). Other aspects of their biology, particularly feeding habits (R.W. Butler, pers. commun.) and reproductive and incubating behaviour (I. Moul, pers. commun.), are currently under study. Herons are relatively long-lived (up to 15 yr) and can accumulate elevated levels of pollutants without suffering toxicological effects; consequently, changes in pollution level over time can be readily detected. Herons are not migratory in the southern mainland or on Vancouver Island, so that, in general, contaminants in the herons reflect qualitative and quantitative conditions in the strait. More than that, based on the quantitative differences in contaminants found among the colonies in this study, each colony is an indicator of pollution in a specific site on the strait.

The survey of organochlorine levels in 1977–79 shows that PCBs were quantitatively the dominant residue in all the eggs. The highest median levels were found in UBC eggs, followed by Coquitlam eggs, reflecting the PCB contamination of biota (Albright *et al.* 1975) in the lower Fraser River and estuary where the birds forage (Paine 1972). Median PCB levels in eggs from colonies away from the Fraser River estuary were relatively low, although some individual eggs carried a substantial burden, e.g., 33.2 $mg \cdot kg^{-1}$ in a Pender Harbour egg. This may be a consequence of the occasional switching of colonies by adult herons (Simpson 1984). PCBs are considered acutely toxic when levels exceed 200 $mg \cdot kg^{-1}$ (Noble and Elliott 1986), considerably higher than the highest individual level (77.5 $mg \cdot kg^{-1}$) found in this study. Peakall (1987) observed that PCBs might have been involved in behavioural abnormalities that led to reproductive failure in Herring Gulls (*Larus argentatus*) in the early 1970s. The mean PCB level in poorly reproducing gulls was 1700 $mg \cdot kg^{-1}$ (lipid weight), compared with 700 $mg \cdot kg^{-1}$ in eggs from colonies that reproduced normally. The decline in PCB levels that has taken place during the past 10 yr, shown in Figure 2, reflects restrictions placed on its manufacture and use since the early 1970s.

DDE is the most persistent metabolite of dichlorodiphenyltrichloroethane (DDT) and generally represents about 90% of total DDT compounds in species at the higher trophic levels (Noble and Elliott 1986). The highest median level found—2.01 $mg \cdot kg^{-1}$ at UBC in 1977—is almost five times the level in the heronry at Sechelt, a comparatively unpolluted area of the Strait of Georgia, which raises the possibility that there was at one time a point source of DDT contamination on the lower Fraser River. The consistent decline in DDE levels that has taken place over the past 10 yr suggests that the source has been either eliminated or contained. Use of DDT has been restricted since 1971; however, DDE levels are unlikely to fall much further, as the major source today is believed to be from the atmosphere (Noble and Elliott 1986).

Dieldrin levels measured in heron eggs on the west coast are generally low, with the exception of an egg collected in the Point Roberts colony in 1977 that contained 6.01 $mg \cdot kg^{-1}$, and another collected from UBC in 1987 that contained 1.64 $mg \cdot kg^{-1}$. Embryotoxic effects have been associated with levels as low as 1 $mg \cdot kg^{-1}$ (Potts 1968). Noble and Elliott (1986) reported that dieldrin was apparently not used in British Columbia, and elevated dieldrin levels are considered to be a phenomenon of the east coast of North America. That conclusion is difficult to reconcile with the data presented here. Given the comparatively short time dieldrin persists in the atmosphere (R.J. Norstrom, M. Simon, D.C.G. Muir, and R.E. Schweinburg, unpubl. data) and its half-life in birds (Kan 1978), our data suggest that there might have been a source of contamination on the lower Fraser River or estuary during the 1970s. That conclusion is supported by the steady decline in levels in eggs from the UBC colony over the past 10 yr (Fig. 2). Today, levels in heron eggs collected at Crofton and Sidney Island (Table 3), away from the lower mainland, are among the lowest recorded (Noble and Elliott 1986).

Figure 2
Organochlorine residues in Great Blue Heron eggs, UBC colony, 1977–87



Heptachlor is an agricultural insecticide and also occurs in technical grades of chlordane. Its use today is severely restricted. Levels of heptachlor epoxide, the most persistent metabolite in tissues, are generally low in heron eggs. Although median levels have declined since 1977 at UBC, the highest individual level was found in an egg collected in 1982. Like dieldrin, the highest median levels are generally associated with colonies on the Fraser River estuary.

Oxychlordane is the most persistent metabolite of the insecticide chlordane. The levels found are generally low, and, unlike the other organochlorines reported here, no consistent fall in concentration has occurred over the past 10 yr. Herring Gulls in the Great Lakes (Elliott *et al.* 1988*b*) and seabirds on the east coast (Pearce *et al.* 1989) have shown similar scattered patterns of oxychlordane residues over the past decade. Chlordane use increased after restrictions were placed on DDT in 1971. In 1978, its use was limited to turf insects and termite control; in 1986, all use was restricted.

HCB was used until as late as 1973 as a fungicide. Kan (1978) noted that HCB is especially persistent in poultry. Levels in herons are generally quite uniform throughout the southern Strait of Georgia, irrespective of urban and industrial development, which may reflect the widespread atmospheric distribution of the chemical that is believed to occur (Noble and Elliott 1986). Hallett *et al.* (1982) reported that HCB is a by-product of pulp bleaching. If so, it is difficult to explain the comparatively low levels in eggs collected from Crofton. Herons in that colony forage an intertidal area just a short distance from the outfall of a major pulp and paper mill.

The major source of the pesticide residues found in eggs from Great Blue Heron colonies in the vicinity of the Fraser River estuary was likely pest control products used in urban gardens. A point source could have been the Later Chemical pesticide formulating plant that operated on Sea Island adjacent to the middle arm of the Fraser River for about 30 yr before closing in 1978. Soil at the site and runoff water were highly contaminated with DDT and its metabolites, as well as dieldrin, heptachlor, chlordane, HCB, and several other pesticides. The high residue levels were caused by spills when chemicals were mixed outdoors, water used to wash processing equipment, and rainwater washing down containers and equipment stored outdoors on the site. The combined runoff drained into the municipal ditch system and eventually ran into the Fraser River.

Whereas levels of several chlorinated hydrocarbons are falling in the Strait of Georgia, as shown by the decline in residues in heron eggs, levels of another family of compounds—dioxins and furans—are increasing in some areas of the strait. Table 4 and Figure 3 show that a striking increase in 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (2378-TCDD) levels in heron eggs from colonies at UBC and Crofton has taken place since 1983. The highest dioxin levels were found in eggs from the Crofton colony in 1987. At the same time, the herons failed to fledge any young. Although the usual complement of eggs was laid, all were

Figure 3
2378-TCDD levels in Great Blue Heron eggs, Crofton and UBC colonies, 1983–87

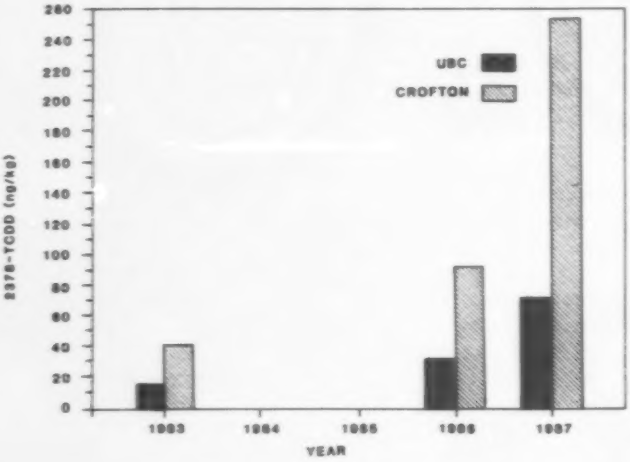


Table 4
PCDD and PCDF levels in Great Blue Heron eggs from British Columbia, 1983–87 (from Elliott *et al.* 1988*a*)

			Residue level (ng·kg^{-1} wet weight), mean ± SD (range in parentheses)[a]							
Location	Year	*n* (in pool)	2378-T4CDD	12378-P5CDD	123678-H6CDD	123789-H6CDD	1234678-H7CDD	OCCD	2378-TCDF	23478-P5CDF
Nicomekl	1983	(7)	7	33	70	ND[b]	6	20	3	15
	1986	5	11 ± 2 (7–12)	32 ± 12 (14–44)	60 ± 35 (21–110)	3 ± 2 (ND–5)	5 ± 4 (ND–9)	2 ± 1 (ND–3)	ND	8 ± 4 (2–10)
Sidney Island	1986	4	11 ± 8 (3–18)	31 ± 22 (9–59)	60 ± 77 (6–174)	5 ± 6 (ND–13)	1 ± 1 (ND–2.5)	ND	1 ± 1 (ND–1)	3 ± 3 (ND–6)
UBC	1983	(10)	15	59	104	ND	6	27	11	48
	1986	7	31 ± 19 (7–63)	94 ± 77 (28–255)	136 ± 119 (40–385)	10 ± 8 (1–23)	18 ± 23 (ND–70)	11 ± 16 (2–47)	5 ± 4 (ND–10)	21 ± 16 (6–51)
	1987	10	71 ± 54 (9–204)	55 ± 28 (23–109)	90 ± 36 (39–158)	6 ± 4 (2–12)	7 ± 4 (2–12)	8 ± 7 (2–19)	22 ± 16 (5–50)	16 ± 5 (9–25)
Crofton	1983	(9)	40	347	911	46	8	25	24	46
	1986	10	92 ± 68 (8–218)	388 ± 315 (11–1018)	544 ± 427 (13–1298)	35 ± 28 (1–89)	4 ± 4 (ND–11)	6 ± 6 (ND–21)	5 ± 5 (ND–14)	30 ± 26 (ND–68)
	1987	10	253 ± 135 (67–444)	314 ± 204 (73–728)	505 ± 293 (110–1052)	31 ± 16 (9–58)	3 ± 1 (ND–4)	4 ± 1 (ND–5)	5 ± 5 (ND–17)	45 ± 26 (10–104)
Gabriola	1983	(8)	22	153	339	23	4	7	11	44

[a] 2378-T4CDD: 2,3,7,8-tetrachlorodibenzodioxin;
12378-P5CDD: 1,2,3,7,8-pentachlorodibenzodioxin;
123678-H6CDD: 1,2,3,6,7,8-hexachlorodibenzodioxin;
123789-H6CDD: 1,2,3,7,8,9-hexachlorodibenzodioxin;
1234678-H7CDD: 1,2,3,4,6,7,8-heptachlorodibenzodioxin;
OCCD: octachlorodibenzodioxin;
2378-TCDF: 2,3,7,8-tetrachlorodibenzofuran;
23478-P5CDF: 2,3,4,7,8-pentachlorodibenzofuran.

[b] ND, no peak observed (signal/noise < 3).

destroyed before they hatched. Dioxins are potent avian embryotoxins (Verrett 1970; Cheung *et al.* 1981). Studies are currently under way to determine if dioxin contamination or some unrelated factor caused the failure.

There are two possible sources of the dioxins and furans contaminating estuarine and coastal areas of the southern Strait of Georgia. About 700 t of chlorophenol formulations are used annually by the forest industry to preserve wood products and protect lumber for export (Garrett and Shrimpton 1988). Those formulations are known to contain a host of dioxins and furans (National Research Council of Canada 1981). For decades, the industry has stacked chlorophenol-treated lumber outdoors without rain protection. Krahn *et al.* (1987) recently reported high levels of chlorophenols in stormwater runoff from lumber mills. As a result, the receiving waters near mills on the Strait of Georgia are often contaminated with chlorophenols (Environmental Protection Service 1979). A second likely source is the kraft pulp and paper mills on the strait. Similar mills are known to produce 2378-TCDD and 2,3,7,8-tetrachlorodibenzofuran (2378-TCDF) in the chlorine bleaching process (Amendola *et al.* 1987). The dioxin output of mills on the strait may be considerably higher than shown by the US study because they commonly use chip stock prepared from chlorophenol-treated lumber.

Our studies of contaminants in Great Blue Heron eggs show that residue levels in colonies on the southern Strait of Georgia are comparatively low. Elliott *et al.* (1989) concluded that organochlorine levels in several seabird species were lower in coastal British Columbia than in California, the Atlantic coast of Canada, and the Great Lakes and were comparable with those in Oregon. Although eggs in all heron colonies sampled on the strait contain the same residues, colonies near urban and industrial areas (UBC, Coquitlam, and Crofton) were more contaminated than those in rural settings (Sechelt, Pender Harbour, and Sidney Island). Finally, residue levels have fallen over the past 10 yr to the point that colonies that once contained high levels are almost as clean today as those in comparatively pristine areas. The decline in residue levels documented here is a positive sign that the estuarine environment in the southern strait is being cleansed of at least some toxic contaminants that had accumulated there in earlier decades. Elliott *et al.* (1989) reported a similar decline in PCB levels in Pelagic Cormorant (*Phalacrocorax pelagicus*) eggs collected from Mandarte Island in the southern Strait of Georgia in 1973 and 1985. The recent discovery of high levels of dioxins in heron eggs underscores the importance of continuing to monitor top-level predators, such as the heron, and serves as a warning against becoming complacent about falling residue levels.

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Overview and recommendations: Important bird habitats and the need for their preservation

Robert W. Butler and Kees Vermeer

1. Overview

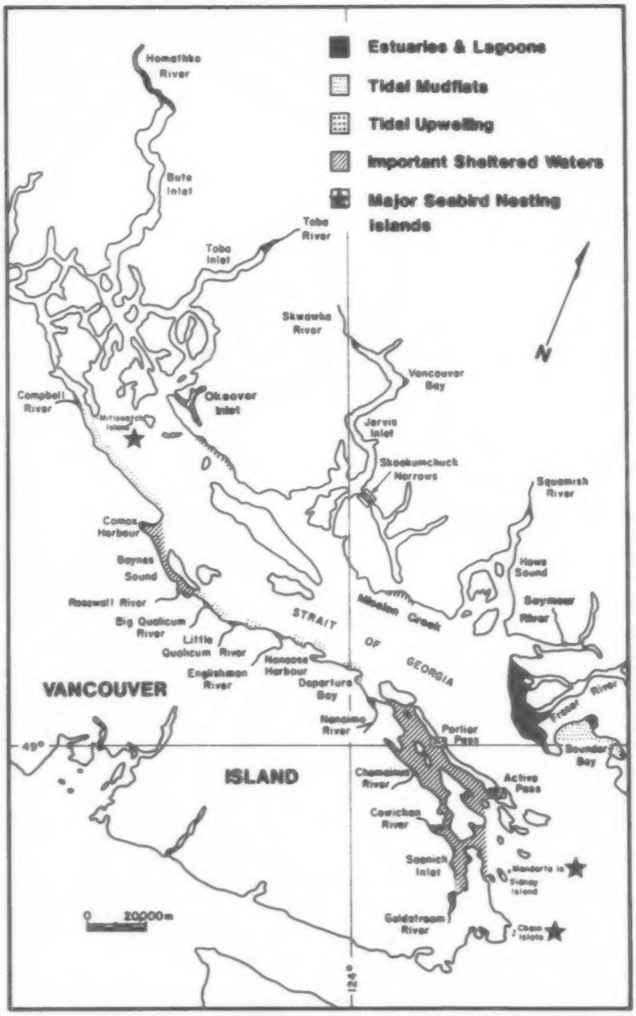
Over 130 species from more than 20 countries and three continents breed, migrate, and/or spend the winter in the Strait of Georgia (Butler and Campbell 1987). Several of those species are present in internationally or nationally significant numbers. For example, most of the world's population of Western Sandpipers (*Calidris mauri*) migrates through the strait (Butler and Kaiser 1988), and all of the Canadian west coast population of Double-crested Cormorants (*Phalacrocorax auritus*) nests along its shores (Vermeer and Rankin 1984).

Large populations of marine and shoreline birds occur in the Strait of Georgia because of the diversity of habitats. We are fortunate that many of the important habitats in the strait are still in good condition. For example, large populations of water birds reside in tidal upwelling areas in Active Pass (Vermeer and Ydenberg, this publication) and along rocky shorelines (Vermeer, Part 3; Vermeer, Morgan, and Smith, Part 3; Emms and Morgan; this publication). However, other important habitats have fared less well.

Between the turn of the century and the 1930s, many estuarine marshes were diked and drained to create farmland. For example, over 75% of the marshes in the Fraser River delta (Butler and Campbell 1987) and about 32% of the former estuarine marshland on Vancouver Island (Campbell-Prentice and Boyd 1988) now lie behind dikes. More recently, marinas, together with forestry activities such as log sorting, lumber storage, sawmills, and pulpmills, have usurped portions of intertidal mudflats and eelgrass beds. Present-day mariculture proposals threaten marine bird habitats (Vermeer and Morgan, this publication). All around the strait, urban development has mushroomed in the past three decades. In addition to habitat loss, increased pollution has degraded some marine and shoreline habitats (Elliott *et al.* 1988; Whitehead, this publication).

Areas known to be important to water birds in the Strait of Georgia (Fig. 1) include estuaries, lagoons, mudflats, tidal upwelling areas, sheltered waters such as bays and inlets, creek mouths, eelgrass beds, algae communities, herring spawn areas, and seabird islands. Many of those areas used by marine and shoreline birds receive the benefits of protection afforded by the Department of Fisheries and Oceans, because fish use similar habitats. However, only a small portion of the Strait of Georgia has been legislated for the preservation of wildlife. Those protected areas include mostly marshes in the Fraser River, Little Qualicum River, Nanaimo River, Rosewall River, and Nanoose/Bonell Creek estuaries. Land use agreements that incorporate wildlife needs have been established for the Squamish and Cowichan river estuaries. Formal arrangements must continue to be made for other marshes, as well as eelgrass and marine algae beds. Some eelgrass beds are

Figure 1
Areas known to be important to marine and shoreline birds in the Strait of Georgia and adjacent waters


■ Estuaries & Lagoons
▨ Tidal Mudflats
▦ Tidal Upwelling
▨ Important Sheltered Waters
★ Major Seabird Nesting Islands
N
Homathko River
Bute Inlet
Toba River
Toba Inlet
Skwawka River
Vancouver Bay
Campbell River
Mitlenatch Island
Okeover Inlet
Jervis Inlet
Shookumchuck Narrows
Squamish River
Comox Harbour
Baynes Sound
Howe Sound
Rosewall River
Seymour River
Big Qualicum River
Little Qualicum River
STRAIT OF GEORGIA
Creek
Nanoose Harbour
Englishman River
Departure Bay
VANCOUVER
Nanaimo River
Fraser River
Porlier Pass
Boundary Bay
49°
ISLAND
Chemainus River
Active Pass
Cowichan River
Saanich Inlet
Mandarte Is.
Sidney Island
0 20000m
Goldstream River
Chain Islets
124°

coincidentally protected because they lie within parks, but none has been legally protected chiefly for its wildlife. Similarly, several seabird nesting islands are protected because they are within parks or Migratory Bird Sanctuaries or because of the presence of research programs. The only mudflat that has received protection chiefly for its wildlife lies in the Shoal Harbour Migratory Bird Sanctuary (Fig. 1). The largest and by far the most important mudflat for birds is Boundary Bay south of Vancouver, but it remains unprotected (Butler *et al.*, this publication). Similarly, no tidal upwelling areas in the Strait of Georgia are protected for wildlife, in spite of their importance to water birds (Vermeer and Morgan, this publication).

Marine ecosystems all over the world are signaling problems. Marine mammals deaths on Atlantic beaches and algae blooms in Scandinavia are only a few of the problems that have been televised and headlined in newspapers. Scientific explanations for their causes are equivocal and underlie how little we understand about biological interactions in these ecosystems. This paucity of information also applies to the Strait of Georgia. Although much biological information has been gathered for the strait, it has in large part not been directed at explaining ecological relationships. If we hope to manage the natural resources in the Strait of Georgia, it is essential to understand its internal workings. We emphasize the need for well-directed interdisciplinary studies for solving and preventing future environmental problems in the strait.

2. Recommendations

The Strait of Georgia supports significant marine and shoreline populations of birds. Their protection requires securing and maintaining adequate habitats. Several major recommendations arising from the papers in this publication should be met if the present populations of water birds in the Strait of Georgia are to be maintained:
(1) The eelgrass and marine algae beds, including those in Boundary Bay, Roberts and Sturgeon banks, Comox Harbour, and Sidney Island, should be secured for their shorebird, waterfowl, and seabird populations (Hutchinson *et al.*; Vermeer, Morgan, Butler, and Smith; Butler *et al.*; this publication).
(2) The marshes in the Fraser, Cowichan, Nanaimo, Squamish, Campbell, Chemainus, and Little Qualicum river estuaries should be preserved for wintering waterfowl (Butler and Verbeek; Butler *et al.*; this publication).
(3) Protection of seabird nesting sites on Chain, Mitlenatch, and Mandarte islands should continue (Vermeer, Part 3; Vermeer and Devito; Vermeer, Morgan, and Smith, Parts 3 and 4; Emms and Morgan; this publication).
(4) Moulting sites for sea ducks, especially postbreeding Harlequin Ducks (*Histrionicus histrionicus*), should be quickly determined and protected from human disturbance (Savard, this publication).
(5) No marine development and harvesting of euphausiids should be allowed at tidal upwelling sites such as Active and Porlier passes and Skookumchuck Narrows prior to a thorough evaluation of the effects of such developments on planktivorous bird populations (Vermeer and Ydenberg; Vermeer and Morgan; this publication).
(6) The sheltered waters outlined in Figure 1 should be secured for marine and shoreline birds (Vermeer and Ydenberg; Verbeek and Butler; Savard; Vermeer, Part 5; Morgan; this publication).

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